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ON THE ISLAND ORIGIN OF THE ENDEMIC TREES OF THE BRITISH GUIANA PENEPLAIN

BY T. A. W. DAVIS, DIP.FOR. (OXON)

(*With one Map in the Text*)

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INTRODUCTION

MANY of the commonest trees in the rain forests of British Guiana are either endemic or confined to the Guiana region. A few have a still more limited range, and occur only in certain groups of hills and their immediate neighbourhood. In other continental tropical regions, e.g. Nigeria, most of the common trees have a wide geographical distribution. Mr Smith Bracewell, the Director of the Geological Survey of British Guiana, and the writer have come independently to the conclusion that the probable explanation why some Guiana trees have such a limited range is that they were once endemic in particular groups of islands at a time when the greater part of the present land surface was submerged, and volcanic islands now represented by hills were the only areas of dry land in the region. If this theory is correct it also explains the distribution of endemic species with a wider range; and its application may be expected to extend to other countries with a similar geological history.

TOPOGRAPHY AND CLIMATE

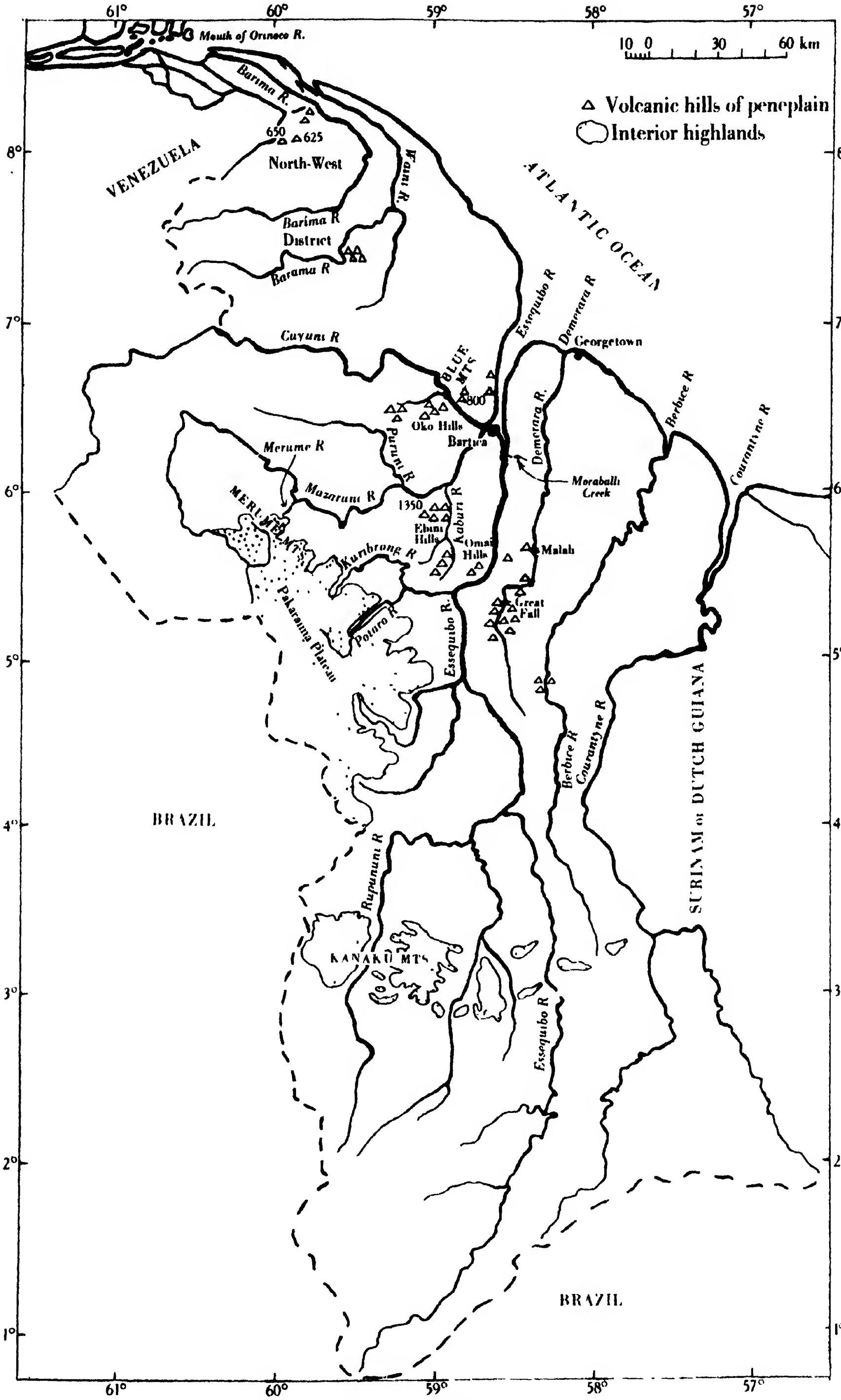
British Guiana is situated on the north-eastern coast of South America between 1° and 8° N. lat. and 57° and 61° W. long., and has a coastline some 430 km. long. The portion of the colony under particular consideration in this paper is a belt of country about 160 km. wide lying immediately behind the very low alluvial coastal plain. It consists for the most part of a sandy peneplain which, on the principal watersheds, is from 75 to 100 m. above sea-level and nowhere exceeds 125 m. Outside British Guiana this plain extends to the

Orinoco River in the north-west and eastwards across Surinam into Cayenne. The basement rocks underlying it are mainly gneiss and gneissose granite. In the North-West District its surface is generally of brown or yellowish loamy sands. Elsewhere the main watersheds are often capped with white quartz sand, this condition being especially prevalent in the north-central and central districts: yellow or brown loamy sands similar to those of the North-West District are usual on the sides of the valleys below white sand level. The plain is deeply indented by numerous rivers and streams, and the latter frequently rise in deep, steep-sided gullies. Locally the drainage has not penetrated so far into the watersheds, and extensive areas of gently undulating country show the true formation of the peneplain. In the Berbice district the topography is somewhat different. The principal watersheds are flanked by wide level terraces about 60 m. in altitude and consisting of pale yellow clay thinly covered with light brown sand. On the riverwards margin the terraces break down into deep gullies separated from one another by steep-sided, knife-edged, sinuous ridges of clay weathered on the surface to a brownish grey colour. White sands occur commonly over large areas near the coastal plain and locally over smaller areas farther inland, both on the river benches and on the watersheds, but on the latter they appear to be generally shallow.

Hills formed by volcanic intrusions of basic rocks, and rising to heights of 100–400 m., but mostly under 300 m. above the sea, are scattered singly, in groups, or in masses over the peneplain. The lower slopes of the higher hills and the whole of those less than 150 m. in altitude are usually sheeted with lateritic ironstone which often forms wide, flat, or gently sloping terraces near their bases. These terraces are sometimes almost devoid of soil, or they may be thinly covered by gravel. Elsewhere the soil of the hills is generally shallow, and either a stiff loam or clay.

Between the upper Mazaruni and Essequibo Rivers the peneplain is bounded on the west by the abrupt escarpment of the Pakaraima plateau: the Kanaku Mountains and a lower chain of hills which extend eastwards into Surinam form its southern limit. The Pakaraima plateau, which consists of sandstones and conglomerates, has a general altitude of 500–700 m. with higher mountains rising from it much as the hills rise from the lower peneplain. The Kanaku Mountains are granitic. West of the Rupununi River they form a definite range some 500 m. in altitude with peaks rising to 900 m., but from that river eastwards they lose height and consist of isolated mountains scattered over broken country little more than 200 m. in elevation.

Climate. The climate is tropical and remarkably equable. In the forest region the average maximum temperature is 29° C. and the average minimum 22° C., and there is only slight seasonal variation. The average annual rainfall is 2286 mm. or more, well distributed throughout the year but concentrated to



Sketch map of British Guiana.

1·2

some extent in two rainy seasons, one from May to August, the other in December and January. The dry seasons vary somewhat in intensity in different localities. In the eastern districts the rainfall is slightly less than in the western, and the dry season from August to November is both longer and appreciably drier, though the dry period between February and April is less pronounced. The humidity is uniformly high, and in the forest does not fall much below saturation point for more than a few hours during the day even in dry weather. The prevailing wind is the North-East Trade. Hurricanes are unknown, and though local squalls are frequent they are rarely severe enough to do significant damage to the forest: what wind damage does occur is never extensive, and is normally confined to very small areas.

VEGETATION AND ECOLOGY

The vegetation of practically the whole of the peneplain is tropical evergreen rain forest. The botanical composition varies somewhat in different localities, the greatest differences being between the extreme north-western and eastern districts. Many species are distributed throughout, but those most abundant in the north-west are usually much less so, or even absent in the east. Such differences in the relative abundance of the principal trees are readily observed, as the local dominance of a single species is far more pronounced in British Guiana than is usual in tropical rain forest (Wood, 1926). The climatic climax is represented by two fairly distinct and regionally separable associations. The *Eschweilera Sagotiana* (Kakaralli)-*Licania venosa* (Kautaballi) association (Davis & Richards, 1933–4, 117)[1] occupies the north-western and central districts, and is subdivisible: in the North-West District the principal consociation dominants are *Eschweilera Sagotiana* and *Licania venosa*, while smaller areas are dominated by *Catostemma commune* (Baromalli) and *Alexa imperatricis* (Haiariballi); in the Essequibo region *Ocotea Rodiaei* (Greenheart) and *Mora Gonggrijpii* (Morabukea) are the commonest dominants, with a tendency for the former to prevail near the coast, the latter farther inland, while *Eschweilera Sagotiana* and *Licania venosa* remain as abundant subordinate species but are actually dominant over a comparatively small proportion of the country (Wood, 1926). In the eastern districts the dominants characteristic of the association are *Aspidosperma excelsum* (Yaruru), *Swartzia leiocalycina* (Wamara), and *Eperua falcata* (Soft Wallaba), while a considerable, but not major, part of the country is occupied by *Ocotea Rodiaei* and *Mora Gonggrijpii* forest in which the subordinate species are the same as are found in other parts of this region. The two associations meet in the valley of the Demerara River.

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[1] In this paper the vegetation of the coastal and riverine plains and other areas subject to flooding is not considered. The majority of the species found in such localities have a wide range. *Mora excelsa* (Mora) forest (Davis & Richards, 1933–4, 109) belongs to this category.

Wherever the drainage is fairly good and the soil is "coloured" (i.e. not white quartz sand) these associations occupy practically the whole of the British Guiana peneplain and the volcanic hills with which it is studded, the only important exception being found in parts of the Berbice district where *Byrsonima-Trachypogon* savannah (Martyn, 1931) replaces rain forest.

On the white quartz sands the composition of the forest is very distinct. Where it is best developed it has the characters of climax rain forest, but the local dominance of a single species is even more marked than on the coloured soils. The regional changes in the vegetation correspond closely with those already described. In the north central and central districts *Eperua falcata* is usually dominant except in the Mazaruni-Kuribrong-Potaro area, where it is largely replaced by *Dicymbe corymbosa*. In the eastern region *Eperua* forest does not occupy so great a proportion of the white sand country. Where it does occur *Eperua grandiflora* (Ituri Wallaba) is the principal dominant, while *E. falcata* forest is restricted to the comparatively moist sides of valleys. Large areas near the coast support less highly developed forest dominated by *Dimorphandra conjugata* (Dakama) or open scrub (Muri) (Martyn, 1931) with *Houmiri floribunda* dominant, types of vegetation which are very local to the west of the Essequibo River.

The belief that the distribution of the types of forest mentioned above is greatly influenced by climate is supported by a comparison of the ecological status of certain species in the regions occupied by the two associations. Where *Eschweilera-Licania* forest is the climax, *Catostemma fragrans* (Baromalli) and *Swartzia Benthamiana* (Itikibouroballi) are found only on the white sands, but in *Aspidosperma-Swartzia leiocalycina* forest they are equally common on coloured soils. Again, *Eperua falcata* occurs in all consociations of *Eschweilera-Licania* forest, but is by no means abundant in them, whereas it is frequently a principal subordinate species and locally a dominant in *Aspidosperma-Swartzia leiocalycina* forest: on the white sand the almost exclusive dominance it holds in the Essequibo region has been shown to be lost in the eastern districts. These changes in habitat show a preference in each case for a moister and more fertile soil in the drier climate of the eastern region. Furthermore, the lowland forest bordering the northern savannah of the Rupununi district (Davis, 1933), where the rainfall is lower and more definitely seasonal than near the coast, corresponds closely in botanical composition with the *Aspidosperma-Swartzia* association, of which it is probably a regional variation. There is, therefore, every reason to conclude that the slight difference in the climates of the eastern and western regions of British Guiana has a marked influence on the vegetation.

DISTRIBUTIONS OF FORTY COMMON TREES

The local and geographical distributions of forty trees characteristic of one or more of the associations and consociations mentioned in this paper are analysed in the table on pp. 8–9. Though further collecting in neighbouring territories would undoubtedly reduce the number of endemic species, it is safe to assume that a large proportion of them have a very limited range. The trees chosen for inclusion in this list are mainly consociation dominants and their commonest associates. Since much collecting has been done in recent years in Brazil and Surinam it is unlikely that so many of them have been overlooked in those countries. The flora of the country round the mouth of the Orinoco is little known, but is probably very like that of the North-West District of British Guiana, and most of the endemic trees probably occur there also: that of other parts of Venezuela appears to be even less closely related than the Brazilian flora. A longer list which included well-distributed, but less common, trees would show a higher proportion with a wide range in tropical America. The local distribution is taken from the records of valuation and reconnaissance surveys carried out by the Forest Department: the writer has himself taken part in these in every locality given in the table.

No less than three-quarters of the forty trees have been recorded only from the Guianas, and half of these are at present known only from British Guiana. Of the remaining ten species eight occur in Brazil as well as Guiana, while one occurs in Trinidad and another in Tobago: only two can be described as widely distributed in tropical America. An unexpected result of the analysis is that nearly as many species are found only in British Guiana and Cayenne as in British Guiana and Surinam, the numbers being five against six: two more occur in Cayenne and extend into Brazil but are not recorded from Surinam. At first sight this would appear to be a mere accident of collection, but there are reasons why this may not be the case in every instance. *Eschweilera Sagotiana* (Kakaralli), for example, which is so abundant farther west, becomes scarce and local near the Dutch frontier, is apparently absent from Surinam, but reappears in Cayenne. *Ecclinusa sanguinolenta* (Barataballi) is, in British Guiana, most plentiful in the North-West District and absent from the eastern districts: it occurs also in Cayenne and Brazil but not in Surinam. *Swartzia Schomburgkii* (Parakusan) occurs both in British Guiana and Surinam, yet is absent from the eastern half of the British colony. Though the absence from Surinam records of so many species found almost exclusively on white sand soils may be due to a lack of botanical material from such areas, strong evidence remains that common British Guiana trees include not only a number with a very restricted range, but also several with a discontinuous distribution.

On the hills which are scattered over the peneplain the forest is of the same ecological types as in the surrounding plain, but slight differences in the botanical composition are nearly always noticeable: a species may be unusually plentiful or the reverse; or one previously known only from a certain group of hills may reappear in another group. The writer has visited several of these groups in different parts of the country while engaged on valuation and reconnaissance surveys, and has observed several instances of this, but most of them cannot be cited because the trees could not be identified. In the valley of the Demerara River three striking examples were noted. Two of them, *Vouacapoua macropetala* (Sarabebeballi) and *Swartzia Jenmani* (Parakusan),[1] have certainly been recorded only from this locality, while the third, a *Clathrotropis*,[2] is either in the same category, or may also occur in Brazil, but is not known from elsewhere in British or the other Guianas. The *Vouacapoua* and *Clathrotropis* are both abundant, and the former is even a minor consociation dominant, in the hilly area in the neighbourhood of the Great Fall: they occur in less abundance in parts of the peneplain immediately around these hills, but have not been seen elsewhere. *Swartzia Jenmani* is more widely distributed in the Demerara River valley, being common from Malali southwards both in the hills and the peneplain, but it does not occur in the Berbice district to the east, and is replaced by the closely related *S. Schomburgkii* to the west. It seems unreasonable to attribute such extremely limited ranges to the influence of climate, since a species can hardly be so exacting in this respect that, though it competes very successfully with its associates in this restricted locality, it cannot even exist in competition with the same species either in the slightly drier climate to the east or the slightly moister climate to the west. Nor is the soil likely to be the deciding factor, since the examples given occur not only on the heavier soils of the hills but also on the sandy soil of the peneplain. It is necessary, therefore, to examine the geological history and geology of the country in more detail to find a satisfactory explanation.

GEOLOGICAL HISTORY AND GEOLOGY

Much work has still to be done before the general geology of the whole of British Guiana can be understood, but geological surveys carried out in recent years have resulted in the publication of a useful summary for the central region of the peneplain and the Pakaraima plateau (Geological Survey of British Guiana, 1934). The basement formation underlying the peneplain consists of

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[1] *Swartzia Jenmani* is very closely related to *S. Schomburgkii* but is distinguishable in the field since it has both the leaflets and flowers considerably larger. Both are remarkable for having deeply fluted boles consisting of thin, wide, plank-like flanges. They grow to a large size. Similarly fluted *Swartzia* spp. (not identified) have been observed in the North-West and Rupununi Districts, but are quite distinct from the species named here.

[2] Forest Department No. 2459, not definitely identified but may be *C. macrocarpa* Ducke which is a Brazilian species.

Table showing the local and geographical ranges of 40 common trees

Explanation. The common names of the trees are Arawak Indian, except those beginning with a small letter which are English. v.a. = very abundant, a. = abundant, *f.* = frequent, o. = occasional, r. = rare. An asterisk against a letter indicates that the species is, in the region indicated, practically confined to white quartz sand areas: † that it is only found in a part of the region.

Species	Distribution and frequency of occurrence in British Guiana					Geographical range
	North-West District	Cuyuni-Mazaruni-Essequibo region	Demerara River region	Berbice River region	Rupununi District (lowlands)	
Catostemma commune Sandwith, Baromalli	v.a.	v.a.	a.	o.	—	Endemic
Licania buxifolia Sandwith, Marishiballi	—	v.a.*	a.*	f.*	—	,,
Licania laxiflora Fritsch, Kauta	f.	a.	r.	r.	—	,,
Licania venosa Rusby, Kautaballi	v.a.	v.a.	a.	o.	—	Eastern Venezuela (mouth of Orinoco River)
Alexa imperatricis (Schomb.), Haiariballi	v.a.	—	—	—	—	Endemic
Alexa sp. undescribed, Haiariballi	—	f.	r.	—	—	,,
Swartzia Jenmani Sandwith, Parakusan	—	—	a.	—	—	,,
Swartzia leiocalycina Bth., Wamara	r.	a.	v.a.	v.a.	v.a.	,,
Vouacapoua macropetala Sandwith, Sarabebeballi	—	—	v.a.	—	—	,,
Cassia pteridophylla Sandwith,† Immirimiaballi	—	v.a.*	a.*	f.*	—	,,
Sandwithia guianensis Lanjouw	v.a.	v.a.	a.	f.	?	,,
Talisia squarrosa Radlk., Moroballi	—	v.a.*	v.a.*	v.a.*	—	,,
Ecclinusa psilophylla Sandwith, Barata	—	v.a.*	v.a.*	v.a.*	—	,,
Pouteria demerarae Sandwith, Assipoko	a.	a.	o.	—	—	,,
Aspidosperma excelsum Bth., Yaruru	f.	a.	v.a.	v.a.	v.a.	,,
Ocotea Rodiaei (Schomb.), greenheart	r.	v.a.	v.a.	v.a.	r.	Surinam
Unonopsis glaucopetala R. E. Fries, Arara	a.	a.	f.	—	—	,,
Licania densiflora Kleinh., Marishiballi	a.	a.	f.	f.	v.a.	,,

Swartzia Schomburgkii Bth., Parakusan	a.†	a.	—	—	—	,,
Dimorphandra conjugata (Splitg.), Dakama	—	o.*	v.a.*	v.a.*	—	,,
Mora Gonggrijpii (Kleinh.), Morabukea	o.	v.a.	v.a.	v.a.	—	,,
Paypayrola longifolia Tul., Adebero	v.a.	v.a.	v.a.	a.	—	Cayenne
Catostemma fragrans Bth., Baromalli	—	v.a.*	v a.	a.	a.	,,
Eschweilera Sagotiana Miers, Kakaralli	v.a.	v.a.	a.	o.-f.	—	,,
Licania majuscula Sagot, Kautaballi	—	—	f.	v.a.	v.a.	,,
Licania heteromorpha Bth., var. perplexans Sandwith, Kairiballi	v.a.	v.a.	v.a.	a.	—	,,
Eschweilera corrugata Miers, Wena Kakaralli	f.	f.	f.	f.	r.	Surinam, Cayenne
Swartzia Benthamiana Miq., Itikibouroballi	—	a.*	f.	f.	—	,,
Eperua grandiflora Aubl., Ituri Wallaba	—	a.*	v.a.*	v.a.*	—	,,
Ecclinusa guianensis Eyma, Barataballi	—	—	o.	o.	f.	,,
Ormosia Coutinhoi Ducke, Korokororo	—	v.a.*	v.a.*	a.*	—	Cayenne, Para (Brazil)
Eperua falcata Aubl., Soft Wallaba	f.	f.-v.a.*	v.a.	v.a.	—	Surinam, Cayenne, North Pará
Dicymbe corymbosa Spruce, "clump wallaba"	—	v.a.*	—	—	—	Rio Uaupés (West Brazil)
Ecclinusa sanguinolenta (Pierre), Barataballi	v.a.	f.	—	—	—	Cayenne, Amazonian Brazil
Sterculia pruriens K. Schum., maho	a.	a.	a.	a.	o.	Surinam, Cayenne, Brazil
Bocageopsis multiflora (Mart.), Arara	—	—	f.	f.	a.	Brazil
Eschweilera decolorans Sandwith, Kakaralli	v.a.	v.a.	f.	o.	—	Tobago
Eschweilera subglandulosa Miers, Kakaralli	—	—	o.	o.	v.a.	Surinam, Cayenne, Trinidad
Pentaclethra macroloba (Willd.), trysil	v.a.	v a.	a.	r.	—	Widely distributed in tropical America
Pouteria Caimito Radlk., Assipokoballi	o.	o.	o.	o.	r.	Widely distributed in tropical America

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† This species is sometimes regarded as a variety (*pteridophylla* (Sandwith) Ducke) of *C. adiantifolia* Spruce ex Bth., a species found in Brazil (Amazonas, Pará).

gneisses and schists, the former predominating; gneissose granites intruded towards the end of the Archean period. Early in the Pre-Cambrian epoch volcanic activity caused acid, intermediate, and basic lavas and ashes to be deposited, and there were minor intrusions. Later, non-foliated granites intruded, and after considerable erosion and partial planation had taken place, the deposition of pink shales, porphyries, and agglomerates in the upper Puruni and Mazaruni districts followed. During a long period of erosion the volcanic schists and granitic mountains were planed down to an undulating surface like that of the peneplain to-day, and on this the Kaieteurian sandstones and conglomerates were laid down, possibly as late as the Cretaceous period, but more probably in the Torridonian. This now forms the Pakaraima plateau which lies to the west of the lower peneplain in the Mazaruni-Essequibo region, and rises from the plain as an abrupt escarpment which formed the coastline as recently, perhaps, as late Tertiary times. Major intrusions of dolerite and norite followed the deposition of the Kaieteurian series.

The sandstone which overlay the country bordering the escarpment was gradually removed and the basement rocks were planed down to a surface of low relief by river action or wave attack. Drainage from the sandstone plateau passed over this surface and left river sand and gravels in the depressions. The peneplain then sank below sea-level and formed a shallow coastal sea, studded with islands some 300 m. or more above sea-level. In the earlier stages of subsidence white clay accumulated in hollows, succeeded by banks of yellow or brown loamy sands. Many of the islands were of basic rocks and became coated with lateritic ironstone which also extended over alluvial or wave-cut beaches fringing them. Other islands were granitic and did not weather to laterite, but crumbled away almost to sea-level, contributing to the white quartz sand which gradually filled the sea and extended from island to island, covering the white clay and coloured sands. The extent of the sea is not known, but the white quartz sands do not occur at the present day in the North-West District or in certain parts of the Cuyuni, Mazaruni, and Essequibo Rivers where the surface of the plain is below white-sand level. Recent seaward tilting submerged the outer part of the white sand, and the coastal mud and sand plain was deposited on this. The last change was the uplifting of the sand-covered land to a height, near the escarpment, of 125 m. This occurred in late Tertiary or Quaternary times. Since then the present rivers have eroded their valleys to give the topography of to-day.

DISCUSSION AND CONCLUSIONS

It has been shown that most of the common trees of the peneplain are confined to the Guiana region comprised by the British, Dutch, and French colonies and adjacent parts of eastern Venezuela. It is therefore likely that there was, in early geological times, a centre of evolution here in which many species (and perhaps a few genera) were developed. The question arises whether the development took place in the mountains and highlands which form its western and southern boundaries or on the present site of the plain. Unfortunately, not much is known of the forest flora of these highlands, since most travellers to such remote places have collected chiefly riparian species, which afford little indication of the botanical composition of the climax association of a region. What little is known of the floras of the Pakaraima plateau and the Kanaku mountains suggests that they have contributed very few species, and those, at least in the case of the Pakaraimas, chiefly to areas near the escarpment, a good example being *Dicymbe corymbosa*. The writer has himself spent a few days in each of several widely separated localities in the Kanakus, and received the impression that the forests were remarkably diversified in composition but had little in common with those of the peneplain. Such species as occur in both the highlands and the peneplain are not very abundant in either, and even the lowland forest country immediately to the north of the mountains has a very distinct vegetation. The trees from the Kanakus represented in collections suggest a close relationship with the Amazonian flora (Davis, 1936).

The possibility of the Guiana flora having evolved where it flourishes to-day must now be considered. Before the plain was submerged in late Tertiary times it presented a surface of low relief with scattered volcanic hills of which only those formed by the harder basic and intermediate rocks survived the subsidence, as islands; on these most of the species now represented in the vegetation of the country as a whole must have been preserved. That some should be saved only on certain islands is to be expected, and would account satisfactorily for the erratic and very limited distribution of several species. Our knowledge, admittedly rather meagre, of the floras of adjacent territories weighs against the supposition that the country was colonized to more than a limited extent by migrations from outside. The available evidence, therefore, leads to the conclusion that the existing vegetation spread over the peneplain from its refuge in the volcanic hills. Beyond that its origin is less certain. The ancient geological history is too imperfectly known to give a reasonable indication whether it originated in the lowlands before they were last submerged, in the hills which may have been islands for one or more long epochs before the most recent period of subsidence of the peneplain, or partly in both. The well-known fact that the isolation of living organisms on islands has a tendency to stimulate the evolution of races and species favours, but does not prove, the theory that the volcanic islands now represented by hills were the actual centres in which the endemic species of the Guiana flora had their origin.

SUMMARY

1. The situation, topography, and climate of British Guiana are briefly described.

2. The distribution of the principal climatic and edaphic associations *(excluding the swamp vegetation or hydrosere) is discussed, and the influence of climate on the distribution of certain species is indicated.*

3. The prevalence of endemism in the Guiana flora is shown by analysing the local and general range of forty of the commonest trees: the erratic distribution of a few of them is discussed.

4. Examples are given of species whose known range is confined to a single river valley.

5. The geological history and geology of the country are examined: it is shown that the peneplain formed the bed of a shallow sea as recently as late Tertiary times, and that this sea was studded with volcanic islands; also that the peneplain was elevated to its present level perhaps as recently as the Quaternary age.

6. The likelihood of the endemic species of the Guiana flora having been evolved in the highlands bordering the western and southern limits of the peneplain is examined and rejected.

7. The conclusions reached are: (1) that the endemic trees of the peneplain originated where they are found to-day; (2) that they were saved from destruction, during the last period of subsidence of the land, on volcanic islands now represented by hills; (3) that they thence recolonized the plain on its elevation to its present level; (4) that the evidence is insufficient to decide whether they were evolved on the plain itself before the last period of subsidence, or on the hills when they were islands during some earlier epoch, though the latter view is favoured.

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THE EFFECT OF VOLES (*MICROTUS AGRESTIS*) ON VEGETATION

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(*With Plates* 1 *and* 2 *and five Figures in the Text*)

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1. INTRODUCTION

FOR some time now it has been known that many (perhaps all) animals exhibit periodic fluctuations in numbers, and in a few cases the actual periods have been worked out by careful examination of collected data. An animal whose fluctuations have received a considerable amount of attention in this country is the common field vole, *Microtus agrestis*. The fluctuations, as has been shown by recent investigations, tend to follow a three- to four-year cycle, and sometimes result in a "plague" at the period of maximum numbers. Such "plagues" as those of 1875–6 and 1891–2 ravaged the sheep pastures of the lowland hills of Scotland. From observations in the field and investigations carried on in the laboratory (see Davis, p. 235) it is clear that the voles consume large quantities of vegetable food, and it was therefore thought probable that this might have a more or less definite effect on the vegetation of the districts inhabited by the voles, especially at the times of vole maxima. I was therefore asked by Mr Charles Elton, Director of the Bureau of Animal Population, Oxford University, who has been directing the research work on vole fluctuations in this country, to carry out a series of experiments in order to see if it were possible to detect and to measure this vole effect on the vegetation. This formed part of a scheme of research on voles financed by a grant to Mr Elton from the Darwin Fund of the Royal Society, and later by a grant from the Forestry Commission.

Two areas were chosen for carrying out the work, both having been already the scene of work on vole fluctuations. There was therefore a considerable body of data available as to previous conditions, while in addition other investigations were being carried on concurrently with that here described. The two areas are both on land which has been or is being planted by the Forestry Commission. The first is in the State Forest of Newcastleton, in the southern part of Roxburghshire, near the English border, the second in the State Forest of Corris, about five miles north of Machynlleth, in the county of Merioneth. It should be noted that the work was carried out during about ten days each July, the vegetation therefore being in a comparable state at each annual visit. The small amount of time available each year has set the limits to the work which could be attempted and determined the character of the survey carried out. The experiments were started in July 1932 and have been continued annually since.

Specimens of all the plants occurring on the experimental plots and of many others in the adjacent communities were collected and are deposited in the Herbarium of the Royal Botanic Gardens, Kew. The names adopted in this account are usually in accordance with the most recent research on each group concerned and do not necessarily follow any standard British Flora or List. The specimens should be consulted in any case of doubt.

2. ACKNOWLEDGEMENTS

I should like in the first place to express my indebtedness to the Forestry Commission without whose interest the successful prosecution of the work would not have been possible. My thanks are due to the various officials of the Commission in the areas concerned and especially to the two Foresters, Mr J. F. MacIntyre at Newcastleton and Mr J. Lomas at Corris. Their unstinted aid in the setting up and maintenance of the experimental plots and profound knowledge of local conditions have been of very great value. For geological data relating to the Newcastleton area I am indebted to Mr D. F. W. Baden-Powell. I should also like to express my grateful thanks to those members of the staff of the Bureau of Animal Population who have helped me in the recording of data and in charting transects, etc., namely, Messrs Charles Elton, D. H. S. Davies, A. D. Middleton and D. Chitty, and to Dr J. R. Carpenter and Mrs E. J. Elton for similar help. I am also indebted to the Meteorological Office for the rainfall data mentioned in this account. The photographs were all taken by Mr Elton.

3. METHODS

The general method adopted was to enclose certain small areas so that voles could not gain access to the vegetation, the resident voles then being trapped out until the areas were vole-free. The vegetation was then compared at regular intervals of time during two vole cycles with similar areas which had remained exposed to vole attack. These experimental areas are termed "quadrats" in the following account.

(*a*) *The cages*

For this purpose a number of small enclosures (referred to as "cages" hereafter) were erected in the spring of 1932 at suitable spots so as to include samples of all the most important communities inhabited by voles (see Fig. 1). These cages are in the form of rectangles 8 yd. long by 4 yd. wide and are surrounded by a 6 ft. fence of ⅜ in. mesh wire netting, the lower 1½ ft. of which are buried in the ground so that it is impossible for voles to enter by tunnelling as they never penetrate so deep as the bottom of the wire. Examination showed that after the initial vole-population of the cages had been trapped they remain quite free from voles for a number of years. No traces of voles could be found, either in the form of excreta or of plant cuttings, in any of the cages until 1937 although such were almost invariably detected each year in the controls and in the vegetation surrounding the cages. The cages are open at the top, access being obtained by climbing over the fence by a stile, so that there is no break in the fence. The wire netting is supported by six strong posts reinforced with wire struts and additional posts on both long and short sides. The controls (see Fig. 2) consist of equal-sized areas with a wire strand around to keep off passers-by but with no wire netting. This was omitted owing to the cost, although its presence in the cages and absence from the controls may have made some slight difference to the vegetation. Although there are a few roe-deer and a small number of rabbits in the forests no traces of them were seen in the controls and they can be neglected. Unfortunately, some sheep gained access from the open sheep pasture at Newcastleton in 1936 and visited the control to one of the cages there (no. 4), but there is no evidence that the visit affected the vegetation to any significant extent although the excreta may have some small effect in subsequent years.

(*b*) *Sampling*

All the communities studied consist mainly of grasses or grass-like plants growing either in a more or less close sward or forming a kind of tussock complex. No accurate method of charting close grassland communities has yet been devised, and even for the charting of tussock-grassland a great deal of disturbance of the ground is necessary. It was, however, essential in the present investigation to disturb the ground to the minimum extent possible in order not to interfere with the vole runs and the general effects produced by the voles. The ordinary methods of large-scale mapping or quadrat charting were therefore quite impracticable. In order to gain an idea of the general changes going on it was consequently decided to take a series of "point" samples by modifying a method which had been tried successfully during a vegetation survey of Richmond Park by the author and some of his colleagues.

The method adopted during the work here described was to lay down a series of lines lengthways along the cages at intervals of 1 ft. and then to take "pinch samples" of the vegetation at 1 ft. intervals along each line. Eight lines were usually taken, four on each side of a central path which was required to obtain access to the whole of the cage. An examination of Fig. 1 will show that there is a space of at least 1 ft. between lines 4 and 5 and the central path. Twenty-two or twenty-three samples were usually taken along each line, the total number of samples per cage being therefore about 180.

In the controls the same general method was adopted except that as the areas can be approached and sampled from the outside (there being no wire netting) there was no necessity for a central path. The lines were therefore laid out at foot intervals on each side of a median line joining two fixed points, one at each end (*A* and *B* in Fig. 2). The number of samples taken in each control was about the same as in the cages (seven lines with twenty-six samples in each line).

The "pinch" sample consists of the amount which can be obtained by opening the fingers and thumb to about $\frac{3}{4}$ in. apart and then closing them so that the included vegetation is pulled out or broken off. Rooted or basal parts only are counted, the pinch being taken at the soil surface. When sampling great care was taken to tread in as few places as possible so as to interfere to a minimum extent with vole runs and the vegetation generally. Apart from these footmarks only the areas of the individual samples (about $\frac{3}{4}$ in. square each) are disturbed, and the interference is much less than in any ordinary type of charting. The placing of the samples at 1 ft. intervals allows a large area to be sampled fairly thoroughly without an excessive number of samples being taken, an important consideration when only a limited amount of time is available.

The presence of each species in a sample was counted as one occurrence, the total of occurrences giving the frequency of the species. These totals are expressed as percentages of the total number of samples. It is thus possible to obtain an idea of the vegetation over the whole of each area sampled, while the small size of the individual samples enables differentiation between species frequencies to become evident. Owing to the regular spacing out of the sampling points the results can be arranged in the form of a map or plan, and this enables the spatial nature of any change to be examined. The necessity of studying the whole of each area was due to the relatively great local variations shown by each community. Owing to the irregularity of these variations it is very unlikely that the regular arrangement of the samples affects any statistical value which the results may possess.

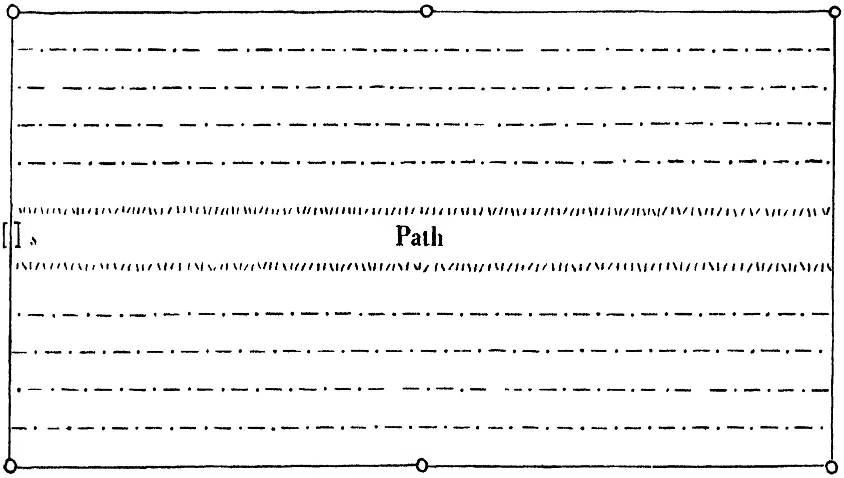


Fig. 1. Diagram of an experimental cage showing the wire-mesh boundary supported by six posts, the stile (*s*) at one end, the central path and the eight lines of samples, four on each side.

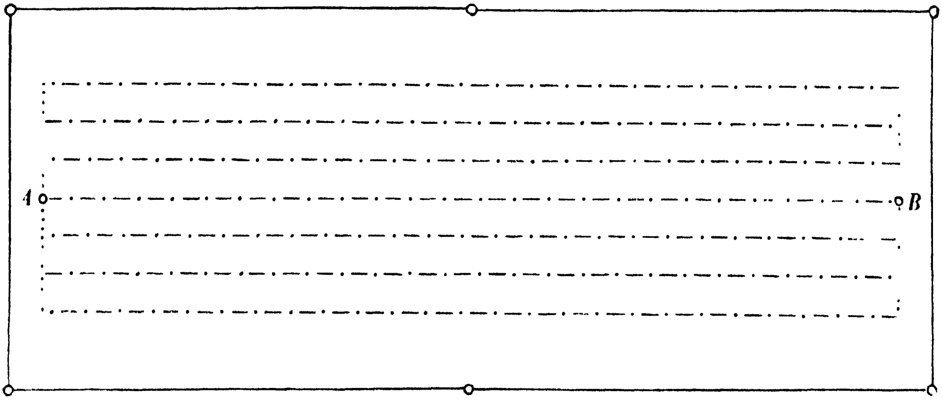


Fig. 2. Diagram of a control quadrat, showing the surrounding wire with supporting posts, and seven lines of samples placed equally on each side of the central base-line which is marked by permanent metal pegs at each end (*A* and *B*).

A difficult matter arising during this method of sampling is the identification of often small scraps of plants, particularly grasses. Close familiarity with all the organs of the species occurring in the areas is necessary in order to obtain certain identification in many instances. In the case of bryophytes, numbered samples of any doubtful or minute portions were kept for microscopic examination later.

Other methods were adopted for measuring certain features of individual species. These will be mentioned later.

4. AREAS STUDIED

(a) *Newcastleton*

A short account of the small mammal fauna of this area and a photograph showing the type of ground has already been published (Elton *et al.* 1935, pp. 279–81). The total forest site, which lies between the Liddel Water and the English border, includes a series of more or less parallel ridges, the crests of which slope gently from north-east to south-west from a maximum altitude of about 1100 ft. (330 m.) in the north to about 700 ft. (210 m.) in the southern part. The deepest valley, that of the Tweeden Burn, has a minimum altitude within the forest of about 500 ft. (150 m.) (see Pl. 1, phot. 1).

Climatically the region lies in the zone intermediate between the Southern Uplands with high precipitation and the drier regions farther south. Rainfall records made at Tweedenhead, which is in the centre of the forest, are as follows for the years 1931–8 respectively: 58·25, 54·33, 39·39, 53·30, 48·76, 47·97, 40·18 and 62·00 in. No great proportion of the total precipitation is in the form of snow, and this snow normally does not persist for any considerable period. The precipitation is generally distributed throughout the year, there being usually an adequate amount during the growing season.

The underlying rock is mostly sandstone of Carboniferous age with layers of limestone, but there are also a few outcrops of basalt. The sides of the valleys are overlain up to 750 ft. (225 m.) altitude with glacial deposits of clay or sand. Above 700 ft. (210 m.) the soil is covered with peat, usually several feet thick and locally very deep. The sandstone and other layers are frequently calcareous. Such areas, where exposed, can be detected by the presence of species which inhabit neutral or calcareous soils and which are not found elsewhere in the forest, e.g. *Briza media*, *Avena pubescens*, *Cynosurus cristatus*, *Linum catharticum*.

Only the most southerly ridge is at present completely planted, the unplanted portions consisting of rough sheep pasture. This varies from *Agrostis*, *Nardus* or *Pteridium* on drier rocky summits or better drained slopes, through *Molinia* grassland on gentler peaty slopes, to wet boggy regions on deeper peat bearing *Calluna*, *Erica Tetralix*, *Scirpus caespitosus* and *Eriophorum* *vaginatum*. Before planting was begun the sheep were removed and subsequently kept off the planted area by enclosure. The result of the removal of grazing and the discontinuance of the associated burning, together with the accompanying improvement in the drainage, has been a great stimulation of growth, particularly as regards *Molinia*, which formed a more or less continuous grassland on peat. Later *Deschampsia caespitosa*, which is not very evident in the original sheep pasture, appeared over large areas bearing glacial deposits.

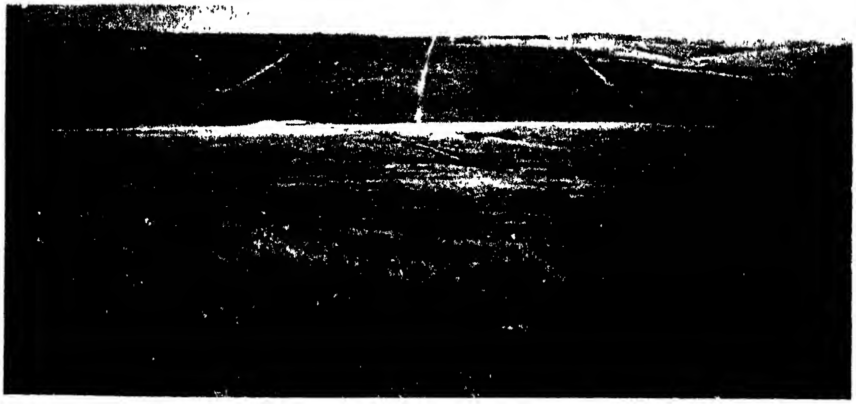
The planted trees consist chiefly of Norway spruce (*Picea Abies*) and Sitka spruce (*Picea sitchensis*), with smaller numbers of Japanese larch (*Larix leptolepis*) and Scots pine (*Pinus sylvestris*). In the early days the young trees exerted very little influence on the natural vegetation, but this has been gradually increasing since then and throughout the duration of the experiment. The cages were placed in a ride running down the north-west slope of the southern ridge about half-a-mile south-west of Tweedenhead, at about 650–750 ft. (195–225 m.) above sea-level (see Pls. 1 and 2, phots. 2–4). At the time they were erected in the spring of 1932 the trees in this district were six years old. A number of trees nearest to the cages and controls were selected and measured giving the following results (see Table 1). It must not be assumed that these figures apply everywhere, since there is considerable local variation in tree growth owing to soil conditions, etc. It will be seen that the trees approximately trebled their heights during the whole period. This is undoubtedly having a great effect not only on the vegetation among the trees but also on that in the rides. On the other hand, the resurveying in 1935 and 1939 of a line transect first surveyed in 1933 did not show any changes, which could be definitely ascribed to the tree effect, in the composition of the vegetation of the horizontally placed ride in which the transect was laid down. (One of the controls is also in this ride.) The ride containing the cages crosses the south-

Table 1. *Average heights of trees in inches (and cm.) at ends of growing seasons for the period* 1931–7

Tree	1931	1932	1933	1934	1935	1936	1937
Norway spruce (40 trees)	33 (84)	40 (102)	45 (105)	57 (145)	64·5 (164)	76·5 (195)	93·5 (238)
Range: in.	15–55·5	18·5–68	21·5–81·5	31·5–99	37·5–114	43–147	50·5–180
cm.	38–141	47–173	55–207	80–252	95–290	109–374	128–458
Sitka spruce (25 trees)	28 (71)	33 (84)	43 (109)	56 5 (144)	60 (152)	70 (178)	82·5 (210)
Range: in.	12·5–47	16·5–59	21–73·5	32–95·5	19*–101	22–116	33–135
cm.	32–119	42–150	53–187	81–242	48–257	56–295	84–344

* The lower minimum and small average increment for Sitka spruce was partly due to deaths and partly to the inclusion of several small trees which had previously been omitted. There was, however, a much smaller average growth during 1935, resulting from the effects of the very severe late frost of 17 May. Compare the increments for the three years 1934–6.

Phot. 1. Newcastleton State Forest, Roxburghshire, July 1937. View up the valley of the Tweeden Burn towards Tweedenhead Farm in the left centre. On the left is [illegible]



Phot. 2. As Phot. 1. View across the valley of the Tweeden Burn from Swarf Hill. On the centre ridge is the forest, the central vertical ride containing the experimental quadrats. In the foreground is unplanted sheep pasture. (Photo C. Elton.)

Phot. 3. Newcastleton State Forest, Roxburghshire, July 1937. Experimental cage 3 seen from the junction of the vertical ride containing the cages with the horizontal ride in which the vole trace censuses are carried out. Behind cage 3 is cage 4, and on the brow of the hill in the background is the control to cage 4. The trees (Norway spruce) are 11 years old and on an average about 2 m. (7 ft.) high. (Photo C. Elton.)

Phot. 4. As Phot. 3. Experimental cage 1, looking down the forested slope towards the Tweeden Burn. In the background, north of the burn, is Swarf Hill, on the slopes of which is unplanted sheep pasture. The spruces by the cage are about 1·5 m. (5 ft. 6 in.). (Photo C. Elton.)

west portion of the regular vole trace-census stake line. There is thus definite information about the vole population of this area. Vole trace censuses carried out through the forest and rides showed virtually no difference in the occupation index of the voles among the trees compared with in the rides. It seems, therefore, that up to September 1936, when these censuses were carried out, the growth of the trees has had no marked effect on the abundance of the voles, except perhaps where the trees had grown particularly well. Censuses taken in September 1937, however, gave higher figures in the rides than among the trees and suggest that immigration was taking place into the rides from the remainder of the forest. An account of the methods used in taking these censuses is being published elsewhere.

The following cages were set up, the plant name indicating the dominant species present:

Cage 1. *Molinia caerulea* (Pl. 2, phot. 4).
Cage 2. *Deschampsia caespitosa.*
Cage 3. *Molinia caerulea* (Pl. 2, phot. 3).
Cage 4. *Holcus mollis.*

Of cages 1 and 3 the latter is relatively pure *Molinia*, whereas in the former there is a greater admixture of other grasses. There are three controls corresponding to the three types of vegetation in the cages. The climate must, on the whole, be comparatively uniform over the limited area containing the cages, while the trees must have exerted much the same effect on all the quadrats except the control to cages 1 and 3 which lies in a wider ride than the others. Here, no doubt, the tree effect has been less marked, particularly during the later years. It should be noted, however, that the severe frost of May 1935 exerted a much more marked effect on the lower part of the slope than higher up so that the trees around cages 1 and 2 were in many cases badly injured while those around cages 3 and 4 were scarcely affected.

The vegetation of the region of the cages consists of alternate patches of *Molinia* and *Deschampsia caespitosa* grassland with smaller patches of *Holcus mollis* and various species of *Juncus*, especially *J. acutiflorus* and *J. effusus*. These latter occur most commonly at the junctions of peat and glacial deposits where springs are formed. There is very great local variation in the vegetation, depending no doubt on the depth of the peat and on the efficacy of the drainage in any given spot. It was consequently not easy within the relatively small areas offered by the rides to choose controls which corresponded even superficially with the vegetation in the cages. The following species have been recorded from the grassland around the cages, either in the rides or among the trees. During the last year or two the growth of the trees has reduced considerably the amount of vegetation outside the rides, but there are local areas where the trees are still small and here the grasses are very tall and thick, reaching to a height of several feet.

Molinia caerulea
Deschampsia caespitosa } l.d.
Holcus mollis

*Achillea Ptarmica
Agrostis canina
A. tenuis
*Angelica sylvestris
Anthoxanthum odoratum
Calluna vulgaris l.
*Cardamine pratensis
Carex leporina
C. panicea
C. stellulata
*Cirsium palustre
Conopodium majus
Deschampsia flexuosa
Dryopteris cristata
*Epilobium palustre
Erica Tetralix l.
Eriophorum angustifolium l.
E. vaginatum l.
*Festuca rubra
F. tenuifolia
*Filipendula Ulmaria
*Galium palustre
Galium saxatile
Holcus lanatus
Juncus acutiflorus
J. conglomeratus
J. effusus
J. squarrosus
Luzula congesta
Poa angustifolia
P. pratensis
Polygala serpyllifolia
Potentilla erecta
P. procumbens
*Ranunculus acris
*R. repens
*Rumex acetosa
Stellaria graminea
Taraxacum officinale (by cage)
Vaccinium Myrtillus
*Veronica Chamaedrys
V. serpyllifolia
Viola? palustris

Species marked with an asterisk are especially characteristic of the areas dominated by *Deschampsia caespitosa.*

The figures obtained by vole trace censuses in the spring and autumn of each of the years 1931–8 are set out in Table 2, and are an index of the fluctuations in numbers during the period. From this it is evident that voles were abundant during the first two years of the experiment (1932 and 1933), but that a low minimum was reached during 1935 and 1936. Indeed it was very difficult to find any traces of voles on the controls during this period, although such were easily observable during the earlier years, as also in the second maximum of 1937–8, the effects of which are described later.

Table 2. *Vole trace census figures at Newcastleton for* 1931-8. *The numbers represent the percentage of over* 150 *sample patches containing fresh dung.* A., April; S., September.

1931		1932		1933		1934		1935		1936		1937			1938	
A.	S.	A.	S.	A.	S.	A.	S.	A.	S.	A.	S.	A.	S.		A.	S.
85	62	17	49	22	76	38	27	6	11	2	11	12	73*	(48†)	29	50

* This high figure is probably caused by the voles having been driven from the forest into the rides by the increasing tree growth.

† Among the trees, for comparison.

(*b*) *Corris*

The forest here occupies both sides of the valley of the Afon Dulas for some distance south of Corris village. The country west of the valley consists of a number of more or less parallel ridges running down from the main ridge Taren y Gesail. The planted area extends from below the summit of this ridge at about 1300 ft. (390 m.) altitude down to the road in the main valley. The slopes near the road and along the lateral valleys are relatively steep and in places rocky, but along the crests of the ridges there are often gently sloping areas, and here there is a considerable depth of peat overlying the Ordovician slates which are so striking a feature of this district.

No exact rainfall data for the forest are available, but records from the three nearest meteorological stations are given in Table 3. It will be seen from the table that the region as a whole has a considerably greater precipitation than that at Newcastleton. There is also no doubt that the precipitation on the planted slopes is much greater than at the lower-lying recording stations. A great deal of the rain falls during the growing season (May–August), there having been several monthly totals of 7–10 in. in the summers under consideration.

Table 3. *Rainfall at three stations near Corris*

	Annual rainfall in in. and cm. (in brackets)				
Station	1931	1932	1933	1934	1935
Tal-y-llyn (280 ft., 85 m.)	82·3 (209)	68·0 (173)	48·8 (124)	—	—
Machynlleth (150 ft., 49 m.)	—	66·4 (169)	54·8 (140)	74·5 (190)	78·6 (200)
Cemmaes (125 ft., 41 m.)	—	56·1 (143)	38·1 (97)	53·7 (137)	60·8 (155)

On the steeper slopes the original vegetation is *Pteridium* or a mixture of grasses, *Vaccinium Myrtillus* and *Ulex Gallii* with *Erica cinerea* on south-west slopes. On the gentler slopes occur *Molinia*, *Scirpus caespitosus*, *Erica Tetralix* and other bog-inhabiting species. The whole before enclosure was sheep pasture, and even now the sheep graze right up to the boundary fences. As at Newcastleton the removal of the sheep, the cessation of burning and the improved drainage have been followed by a great increase in the luxuriance of the vegetation, the *Molinia* especially being particularly dense and well grown.

Several species of trees have been planted on the lower slopes, but higher up, especially where there is any depth of peat, spruces (Norway and Sitka) and to a less extent Japanese larch are the main trees. As at Newcastleton, the growth has been rather irregular, depending on local conditions of soil and exposure. The cages and controls were placed on the lateral ridge Taren Cadian, in a shallow col between a small hill and the next higher point of the ridge, at about 950 ft. (285 m.) altitude. The ground here is almost flat, but slopes steeply on each side to the valleys of the Cwm Cadian and Nant y Coedwig streams. The trees in this district were 3–4 years of age when the cages were set up. Measurements of selected trees near the cages and controls during the period of the experiment give the figures in Table 4 (all the trees concerned are

Sitka spruce, 24 trees). It will be seen that the average height of the trees at the end of 1931 was somewhat less than that of the Sitka spruces at Newcastleton, but that the trees subsequently made rather better growth. The above figures, however, do not give a true measure of the tree effect at Corris. In the first place the rides are wider than the vertically placed one at Newcastleton containing the cages, and, secondly, in each case at Corris the tree growth opposite the cages and controls on one side of the ride was almost negligible. Until the last year or so the trees therefore have influenced the quadrats from one direction only, and even then from a greater distance than at Newcastleton.

Table 4. *Average heights of trees in inches (and cm.) at ends of growing seasons during the period* 1931–6

	1931	1932	1933	1934	1935	1936
Av. height	26 (66)	34 (86)	43 (109)	55 (140)	68 (173)	82 (208)
Range: in.	8–47·5	11·5–57	14·5–73	17·5–91	21·5–103	27–125
cm.	20–121	29–145	37–186	44–232	54–262	69–318

Two cages (with comparable control areas) were erected in April 1932. Cage 1 lies in almost pure *Molinia* grassland, but cage 2 contains a mixture of *Molinia* and *Deschampsia flexuosa*. The ground here, however, is actually more boggy than in cage 1, with cushions of *Polytrichum commune* and a little *Eriophorum vaginatum*. The vegetation in the immediate vicinity of the cages is much more varied than at Newcastleton, chiefly owing to the greater local differences in slope and exposure. The gentler slopes along the ridge in both directions are occupied by *Molinia*, but there is a strong admixture of *Scirpus caespitosus* and *Erica Tetralix*. *Vaccinium Myrtillus* is also common locally, while *Carex binervis* forms almost pure communities covering small patches. Streams drain from the col down each slope, and here are *Juncus* spp., *Deschampsia caespitosa* and other bog-loving species. A striking feature of the wetter parts is the great abundance of *Narthecium ossifragum*, which forms golden carpets during its flowering period. There are rocky slopes in several directions where *Erica cinerea*, *Vaccinium Myrtillus*, *Ulex Gallii*, *Agrostis* spp., *Festuca rubra* and other species are abundant, while *Pteridium* dominates on less rocky well-drained slopes.

During the period under discussion the voles, as measured by the vole-trace censuses in spring and autumn of each year, fluctuated as shown in Table 5. It will be seen that there was considerable fluctuation annually, but that numbers were highest in 1932. In 1935 and 1936 the spring minima rose somewhat again, but the autumn maximum continued to fall. It is clear that there has been considerable vole pressure during the growing season throughout the whole period of the experiments, although this was highest at the beginning. This contrasts remarkably with the figures already given for Newcastleton.

Table 5. *Vole-trace census figures for* 1932–7 (*percentage of points*)

1932		1933		1934		1935		1936		1937
Apr.	Sept.	Apr.	Sept.	Apr.	Sept.	Apr.	Sept.	Apr.	Sept.	Apr.
67	87	13	51	(18)	48	26	45	26	36	18

5. VOLE ACTION

The action of the voles comes under two main headings, namely, (*a*) cutting and eating the aerial parts of the plants, and (*b*) forming the subsuperficial run system in which they also move about.

(*a*) The voles obtain most of their food from the herbaceous vegetation covering the area, as apparently trees are only attacked when the vole numbers become very high, and not always then. In the course of feeding, the voles cut up stems and leaves into pieces which are left lying either in the open, or more generally in the runs, and which apparently are never eaten. In comparison with the amount eaten the amount left must be relatively small, but it nevertheless represents a considerable loss to the plants and gives a clue to the immense damage done. Some of the cuttings are used in the construction of nests. The true grasses presumably form the staple diet both at Newcastleton and Corris, particularly *Molinia* and *Holcus mollis*, of which cuttings are found in great quantities. *Deschampsia caespitosa* is also often badly attacked, and frequently the whole of an inflorescence several feet high may be found cut up into small pieces. Species of *Juncus*, especially *J. acutiflorus* and *J. effusus*, are often eaten or at least seriously cut up, while other plants of which cuttings have been observed are *Potentilla erecta* (frequently), *Calluna*, *Carex binervis*, *Scirpus caespitosus* and *Vaccinium Myrtillus*. The seeds of *Potentilla* are apparently eaten.

(*b*) The formation of the extremely extensive and complicated system of runs has a profound effect on the vegetation. It results primarily in the destruction of any living plant organs which may occur originally or grow up subsequently in the run. It also appears that the voles gnaw away the tussocks of *Molinia* and other tufted grasses which border the runs. Often the tussocks are found almost completely undercut and can be easily dislodged. In addition to the actual destruction of living organs, the voles remove or keep disturbed the superficial humus layer, allowing greater aeration of the upper layers of the soil and preventing the accumulation of the thick layer of dead leaves which is so characteristic of the cages from which voles have been excluded. In addition to the subsuperficial system of runs, the voles construct deeper runways in the peat or soil which are interconnected over a wide area and affect the drainage.

The effects as described above naturally vary from year to year with the density of the vole population. In seasons of low density the vole action is only evident on careful examination, but in a year of maximum density (such as 1938) the openings of the runs are visible everywhere, while the vegetation layer and upper soil layers are virtually honeycombed with the run system.

6. RESULTS AND DISCUSSION

In Tables 6–11 are set out the results of the sampling, for the years 1932–8 inclusive, of the four cages and controls at Newcastleton and the two cages and controls at Corris. In each table the figures for the respective controls follow those for the cages in each year's column. At the base of each table the totals of some of the more significant groups of species are given, together with the number of blank samples. All figures represent percentage frequencies except those for "Angiosperms (excluding dominant)" which are obtained by adding together the percentage frequencies of all the relevant species. This total may therefore exceed 100 in rare instances. The sign + opposite a species indicates that it was noticed in the area sampled but was not actually taken in any individual sample. In order to show more readily any changes or fluctuations which have occurred, the frequencies of the dominant species and of the groups already mentioned are set out in the form of graphs (see Figs. 3–5).

A comparison of the tables and figures shows a number of interesting features which may be summarized as follows:

(1) During the period the dominants have maintained themselves at about the same level of frequency (as measured by the method used) or have slowly decreased. This is true equally of the cages and of the controls.

(2) The mosses have decreased in a remarkable manner in all the cages, but have maintained themselves or even increased in the controls.

(3) The total angiosperms, excluding dominants, have shown a marked decrease in all the cages except the *Deschampsia* cage at Newcastleton, whereas in the controls the frequencies have been maintained at Newcastleton but have decreased at Corris.

(4) There are clearly considerable fluctuations in the frequencies of the various species and species groups from one year to another.

It will be of interest to consider these four points in further detail and to attempt, so far as possible, to analyse and explain the actual figures.

(1) *The dominants*

Visual observation corroborated the general conclusions mentioned above. The dominant species in each case occupies quite fully the area concerned, and there was no obvious difference noted in any of the quadrats during the period of observation, except in cage 2 at Newcastleton in 1937 and 1938. It will be noticed in the case of *Molinia*, however, that there was a distinct decrease in all the Newcastleton quadrats (cages and controls) during the last few years,

Table 6. *Newcastleton, cage* 1 *and control. Frequencies of species and certain species groups. In each year the figures for the cage are given in the first column, those for the control in the second. A + sign indicates that the species was present but not sampled. The figures for Angiosperms (excluding Molinia) are obtained by adding together the frequencies of all the relevant species.*

Species	1932		1933		1934		1935		1936		1937		1938	
Molinia caerulea	49	56·5	45·5	52	57·5	50·5	55	53·5	46·5	47·5	43	41	42·5	33
Agrostis canina	5	1·5	5	1·5	4·5	5·5	3	4·5	1	3·5	1·5	5	0·5	1
A. tenuis	3	+	6	0·5	4·5	2	3	0·5	3	0·5	4·5	1	4·5	2
Anthoxanthum odoratum	1	2·5	6·5	3·5	6	0·5	3	4	0·5	1·5	1·5	2·5	2·5	+
Carex Goodenowii	—	—	+	—	—	—	—	0·5	—	—	—	0·5	—	—
C. stellulata	—	—	—	—	—	+	—	—	—	—	—	0·5	—	—
Conopodium majus	—		—		+		+		—		—		—	
Deschampsia caespitosa	0·5	0·5	0·5	—	+	—	—	—	—	—	—	—	—	—
D. flexuosa	5		4		6		3		1		0·5		1	
Dryopteris cristata		—		—		—		—		—		—		+
Eriophorum vaginatum	—	—	—	—	—	+	—	+	—	—	—	+	—	+
Festuca tenuifolia	4·5	0·5	5·5	—	6·5	—	2	0·5	1	—	1	1·5	0·5	+
Galium saxatile	20	3·5	10	8	6·5	10	7	25·5	0·5	6	1	7·5	+	6·5
Holcus lanatus	2	—	+	—	0·5	0·5	1	—	+	—	+	—	1	—
H. mollis	—	+	—	2·5	—	4	—	6	—	4·5	—	4·5	—	4·5
Juncus acutiflorus	13	0·5	13·5	1	17	1·5	13	2	9	1	6·5	1	6	1·5
J. conglomeratus	—	0·5	—	—	—	—	—	—	—	—	—	—	—	—
J. effusus	—	+	—	0·5	—	1	—	0·5	—	—	—	1	+	0·5
Luzula congesta	—	—	+	—	—	+	—	—	—	—	—	+	—	+
Poa pratensis	+		—		—		—		1·5		6·5		6	
Potentilla erecta	0·5	2	3	1	5·5		4	1·5	3	0·5	3	2	2	0·5
Rumex acetosa	+		0·5		+		+		+		+		+	
Vaccinium Myrtillus	—		—		—		—		—		+		+	
Mosses	44	17	35·5	12	24·5	20	9	33·5	3	31	—	37	1	36·5
Angiosperms (excl. Molinia)	54·5	11·5	54·5	18·5	57	29	39	45·5	20·5	17·5	26	27	24	16·5
Blank samples	15·5	32·5	20·5	34·5	15	29	25	18·5	42·5	31	42·5	31·5	43·5	37

Table 7. *Newcastleton, cage* 3. *As Table* 6 (*for control see Table* 6)

Species	1932	1933	1934	1935	1936	1937	1938
Molinia caerulea	64·5	58	67·5	58·5	43·5	42·5	45·5
Agrostis canina	4	1·5	1·5	—	0·5	3	1·5
A. tenuis	0·5	—	+	—	+	0·5	0·5
Anthoxanthum odoratum	1	1	0·5	+	+	2	0·5
Carex Goodenowii	+	—	—	—	—	—	—
Deschampsia flexuosa	12·5	8	11·5	3	1	1·5	2
Festuca tenuifolia	11	4·5	5·5	3	1	1	+
Galium saxatile	13·5	14·5	12·5	9	1·5	2·5	4·5
Holcus mollis	1·5	7	9	11·5	16·5	17	19
Juncus acutiflorus	1	0·5	4·5	1	1·5	1	2
Luzula congesta	0·5	—	—	—	+	—	—
Potentilla erecta	5·5	7	4·5	7	4	4·5	1·5
Mosses	52·5	38	31·5	4·5	2	2	2
Angiosperms (excl. Molinia)	51	44	49·5	34·5	26	33	31·5
Blank samples	11·5	17	12·5	25	38	33·5	33

Table 8. *Newcastleton, cage 2 and control. As in Table 6*

Species	1932		1933		1934		1935		1936		1937		1938	
Deschampsia caespitosa	23	28	24	17	21	21·5	30	27·5	14	18	9	18·5	3	14
Achillea Ptarmica	0·5	—	+	+	+	+	0·5	+	—	+	0·5	0·5	0·5	—
Agrostis canina	1·5	2	—	0·5	—	2·5	0·5	1·5	—	4	—	1	0·5	2·5
A. tenuis	3	0·5	1·5	1·5	+	1	1	2·5	2·5	2·5	5·5	4·5	3·5	2·5
Angelica silvestris	—	—	—	—	—	—	—	—	—	—	+	+	—	+
Anthoxanthum odoratum	3·5	—	3·5	0·5	5·5	—	2·5	1	6·5	1·5	5·5	3·5	5·5	1
Cardamine pratensis	0·5	—	+	0·5	0·5	—	—	+	1	0·5	+	0·5	2	+
Carex leporina	—		—		—		—		+		—		—	
C. panicea		—		—		—		0·5		—		—		—
Cirsium palustre	+	—	+	+	+	+	+	+	+	0·5	+	+	+	0·5
Conopodium majus	+	—	+	—	+	—	0·5	—	0·5	—	0·5	—	0·5	—
Epilobium palustre	—	—	—	—	0·5	—	+	—	+	—	+	—	+	+
Festuca rubra	3·5	1	11	0·5	10	2	17·5	4	15	5·5	24	7	13	2·5
Galium palustre	—	—	+	+	+	—	0·5	—	—	1	+	1	+	0·5
G. saxatile	+	—	—	—	—	+	—	+	0·5	—	—	—	—	0·5
Holcus lanatus	2	—	4·5	+	5	2	7	16·5	6·5	16	12	9	25	15
H. mollis	1·5		1		2		5·5		11		14		10·5	
Juncus acutiflorus	16·5	2	18·5	0·5	12	0·5	13·5	4·5	6·5	2	8	2·5	8	2·5
J. conglomeratus	0·5	1·5	+	+	0·5	—	0·5	2	1	1·5	—	0·5	0·5	2
J. effusus	—	4·5	1	6	4	3·5	1·5	8	1	4	1·5	4	1	4·5
Luzula multiflora		—		+		—		—		—		—		—
Molinia caerulea	0·5	1	—	1·5	2·5	2·5	0·5	1·5	0·5	0·5	—	1·5	—	0·5
Poa pratensis	—	—	—	—	2	—	2·5	—	1·5	—	5·5	0·5	11·5	0·5
Potentilla erecta	3·5	4	2	2·5	4	2	5	4	5	5	8	3·5	3·5	2
Ranunculus acris	+	—	+	0·5	+	—	+	—	+	—	+	—	—	—
R. repens	+	—	—	—	—	0·5	—	—	—	—	—	—	+	—
Rumex acetosa	4·5	—	2·5	+	0·5	+	+	—	+	—	1	—	+	—
Stellaria graminea	0·5	—	0·5	+	+	+	—	+	—	+	+	0·5	0·5	—
Taraxacum officinale	—		—		+		—		—		—		—	
Veronica Chamaedrys	1·5		5		2		2		1·5		4·5		0·5	
V. serpyllifolia	1·5		—		—		—		—		—		—	
Viola ? palustris		0·5		—		—		—		—		—		—
Mosses	57	46·5	31	39·5	41	43·5	23	56·5	7·5	62·5	13	51·5	27	55·5
Angiosperms (excl. Deschampsia)	45	17	50	14·5	51	15·5	61	46	60·5	44·5	90·5	40	86·5	37
Blank samples	23	31·5	27	40·5	27·5	38	28·5	16	40	16·5	26·5	23	25·5	28

Table 9. *Newcastleton, cage 4 and control. As in Table 6*

Species	1932		1933		1934		1935		1936		1937	
Holcus mollis	67·5	60	58	42·5	58	60·5	71	81	60	71	62	64·5
Agrostis canina	—		0·5		+		—		—		—	
A. tenuis	5·5	+	2·5	—	3·5	0·5	—	+	1	0·5	+	0·5
Anthoxanthum odoratum	3·5	5	12·5	6·5	13·5	5	3·5	5·5	+	4	1	5·5
Poa pratensis	5				2·5		11		11		13	
Conopodium majus	0·5		—		+		+		+		—	
Deschampsia caespitosa	+		0·5		0·5		+		+		—	
Festuca rubra	11		8		6		7·5		2		0·5	
Galium saxatile		1·5		1		4·5		4		4		6·5
Holcus lanatus	4·5	—	2	1	2	—	1·5	—	0·5	—	0·5	—
Juncus acutiflorus	13	4	6·5	3·5	2	4	2·5	3·5	0·5	1	1	1
Molinia caerulea	6	14·5	4·5	15	4	7	4·5	13	4	6	2	6
Potentilla erecta		1		+		+		+		+		+
Rumex acetosa	0·5		—		—		—		—		+	
Mosses	11	6	11	8	2·5	6·5	2	9·5	0·5	12·5	4·5	17·5
Angiosperms (excl. Holcus)	49·5	26	37	27	34	21	30·5	26	19	15·5	18	19·5
Blank samples	17	23·5	22·5	35	25·5	28·5	21	10	32	21	31	24

Table 10. *Corris, cage* 1 *and control. As in Table* 6

Species	1932		1933		1934		1935		1936		1937		1938	
Molinia caerulea	69	68·5	55·5	57	64	63·5	55·5	70	59·5	71·5	49·5	60	48·5	50
Agrostis canina	1·5	0·5	—	1	+	+	+	1·5	+	0·5	+	0·5	+	0·5
A. tenuis	+	—	+	—	+	—	—	—	+	0·5	+	+	—	+
Anthoxanthum odoratum	—	—	0·5	—	—	—	—	—	0·5	—	+	—	0·5	+
Calluna vulgaris		1		+		—		+		—		—		—
Carex binervis	+	1	+	1	—	—	—	—	—	—	—	—	—	—
C. Goodenowii		—		—		—		—		+		0·5		—
Deschampsia flexuosa	+	1·5	+	1	+	2	+	+	+	+	+	0·5	+	+
Erica cinerea		0·5		—		—		—		—		—		—
E. Tetralix		1		+		1		0·5		+		+		+
Festuca tenuifolia	4	9	1	6	0·5	5·5	+	5·5	+	4·5	+	2·5	+	0·5
Eriophorum vaginatum	+		—		—		—		—		—		—	
Galium saxatile	0·5	0·5	1	—	—	—	—	0·5	—	—	—	—	—	—
Luzula congesta	+	+	+	—	—	+	—	—	—	+	—	—	—	+
Narthecium ossifragum	0·5	5	—	6·5	—	2·5	—	6	—	5	—	0·5	—	0·5
Potentilla erecta	0·5	1	+	+	+	+	+	+	+	+	—	1	—	+
Scirpus caespitosus	3·5	5·5	1·5	4	+	4	+	6	0·5	4·5	+	2·5	—	1·5
Vaccinium Myrtillus		+		1		+		+		+		+		0·5
Mosses	25	26·5	8·5	18	0·5	27·5	1·5	24	—	27	0·5	28	—	27·5
Angiosperms (excl. Molinia)	10·5	26·5	4	20·5	0·5	15	+	20	1	15	+	8	0·5	3·5
Blank samples	20·5	17	37·5	24	35	25·5	44·5	21·5	40·5	18·5	50·5	23·5	51·5	39

Table 11. *Corris, cage 2 and control. As in Table 6*

Species	1932		1933		1934		1935		1936		1937		1938	
Molinia caerulea	57·5	41·5	38	27·5	59	38·5	44·5	31·5	51	41·5	35	27·5	37·5	31
Deschampsia flexuosa	32	56	32·5	35·5	29	34·5	15	34	15	27·5	13·5	28·5	16	17·5
Agrostis canina	6	7	8·5	5·5	6·5	3	0·5	3	2·5	2·5	3·5	4	2·5	2·5
A. tenuis	1	—	2·5	—	0·5	1	2·5	—	1	—	0·5	3	3·5	1
Anthoxanthum odoratum	—	—	—	—	—	—	0·5	—	+	—	+	—	+	1
Calluna vulgaris		+		1		1		+		+		+		—
Carex binervis	—	1·9	1·5	2·5	2·5	2·5	—	1	—	+	—	1	—	—
C. hirta	—		—		0·5		—		—		—		—	
C. stellulata		+		—		—		—		—		—		—
Empetrum nigrum		—		+		—		1		—		—		—
Erica Tetralix	3	6	0·5		1	9	+	3	—	4	—	2·5	—	+
Eriophorum vaginatum	1		0·5		+		—		—		+		—	
Festuca tenuifolia	28	13	13·5	5·54	12	3	3·5	2·5	3·5	1·5	3	+	2·5	1
Galium saxatile	6	2·5	3·5	1·5	5	10	+	12·5	+	10	0·5	17·5	+	26
Juncus? effusus	—		—		—		—		+		—		—	
Luzula congesta	—	+	+	+	+	+	+	+	+	+	+	+	0·5	+
Nardus stricta	—	—	0·5	—	—	+	—	—	—	—	—	1	—	—
Narthecium ossifragum	7	1	4	—	3	—	+	—	+	—	+	—	+	—
Polygala serpyllifolia	—		—		1		—		—		—		—	
Potentilla erecta	4·5	5·5	1·5	1·5	+	1·5	+	1·5	+	+	+	+	+	+
Scirpus caespitosus	4	2·5	3	1	1	+	2·5	1	+	—	+	+	+	+
Sieglingia decumbens	1		1		1		0·5		—		—		—	
Vaccinium Myrtillus	4	9	4	8·5	4	5·5	+	3	+	1·5	+	1·5	—	+
Mosses	92·5	95·5	72	84·5	54·5	91·5	27·5	97	3·5	90	1	84·5	1·5	77
Angiosperms (excl. Molinia)	97·5	104	77	65·5	66	71	25	62·5	22	47	21	59	25	49
Blank samples	0	0	6·5	3	5	3	31·5	1	35	2·5	50	8·5	43	8·5

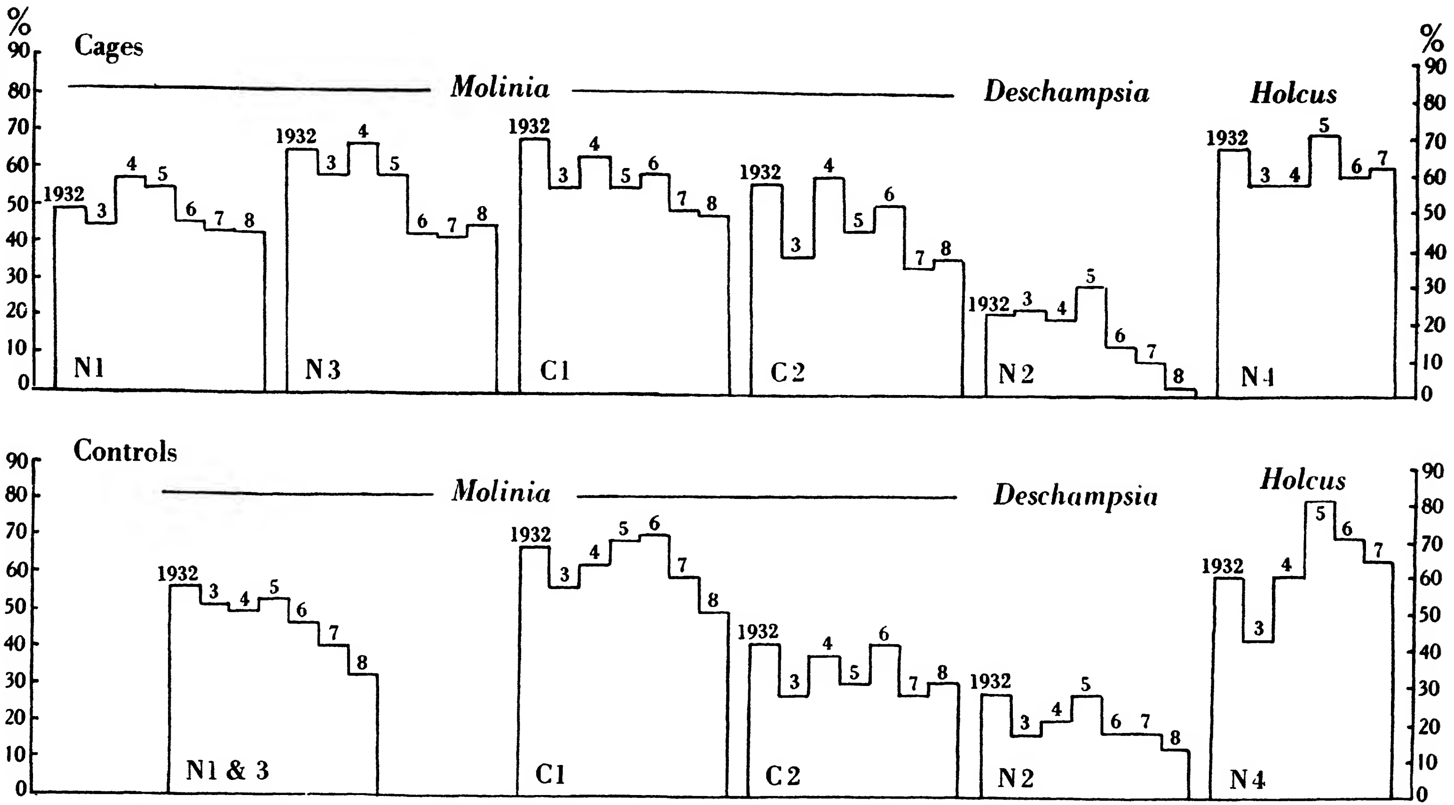


Fig. 3. Diagrams showing percentage occurrences of the dominant grasses in the cages and controls at Newcastleton and Corris during the years 1932–8. Each outline represents a cage or control, the letters N and C referring to Newcastleton and Corris respectively. Each control is placed vertically beneath the corresponding cage or cages. The dominants in each case are indicated above.

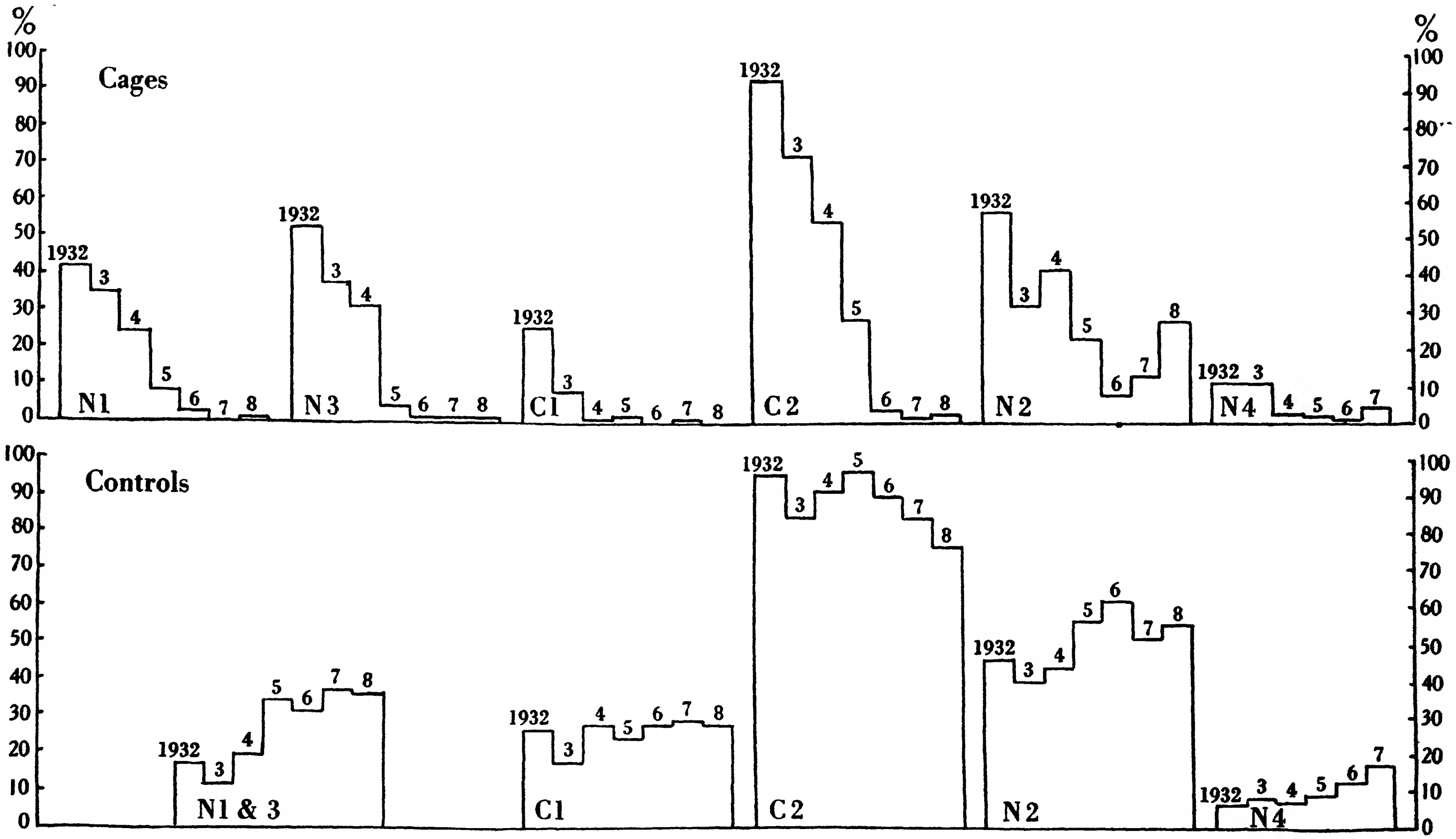


Fig. 4. As in Fig. 3. but showing percentage occurrences of mosses during the same period.

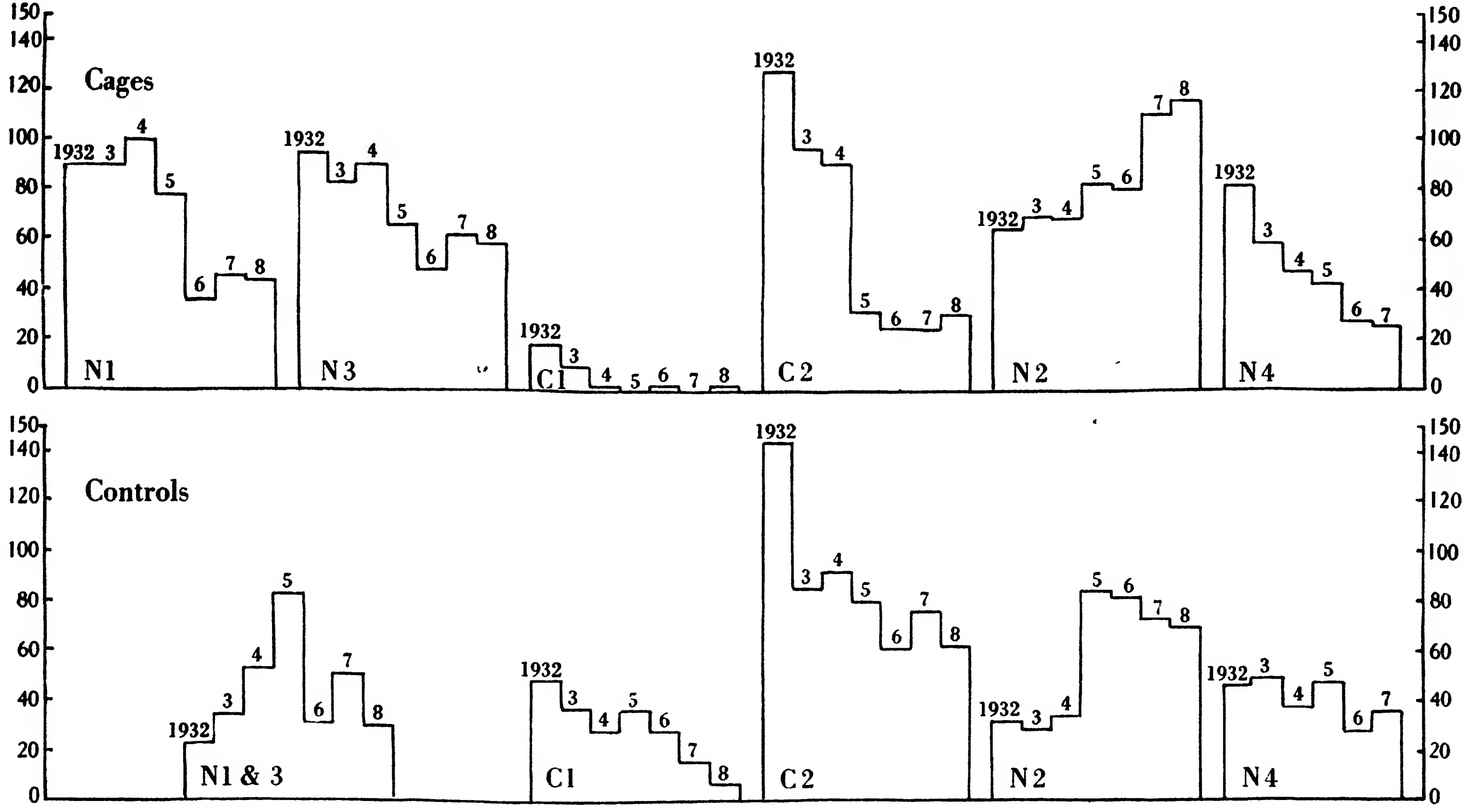


Fig. 5. Total angiosperms apart from dominants. The general arrangement is as in Figs. 3 and 4 but the vertical columns represent the sum of the occurrences of all the species.

but at Corris the decrease is much less obvious. It is almost certain that this is largely due to the competition of the trees, which are very near the edges of the quadrats at Newcastleton, these being placed in a relatively narrow ride. At Corris the trees are not so near the quadrats. This point has already been discussed when considering the growth of the trees.

It therefore appears that the voles did not exert any definite influence on the quantity of the dominants, as shown by the sampling method used, until 1938, since the figures for both cages and controls are similar in the previous years. In 1938 at Newcastleton the dominants exposed to vole attack suffered very badly, this being evident both from the sampling figures and from visual observation. This applies not only to the controls but to the cages containing *Deschampsia* and *Holcus* where the wire had become corroded and broken so as to admit the voles. In September 1937 the vole density was higher than in any other year during the period of the experiments except September 1933, with results on the vegetation which were apparent everywhere in July 1938. Since in the cages the *Molinia* figures show practically no change from the two preceding years, it seems reasonable to suppose that the decline outside the cages was mainly due to the voles. The fact that the effect of the vole maximum of 1938 was much more obvious than that of the maximum of 1933 is possibly due to the weakening action of the tree competition during the intervening years. Admittedly there was a drop in the frequency figures of all the dominants in 1933, but this was not confined to the controls and also occurred at Corris where there was no vole maximum in 1933. In fact other evidence suggests that the dry growing season was responsible for this fall in the frequency figures of the dominants in both places. This is discussed more fully later on (p. 45). It is also possible that the vole concentration in the rides was temporarily much higher in 1938 on account of immigration from surrounding areas. Owing to the fact that the normal trace censuses were carried out in April and September there are unfortunately no exact data for July.

It had been noticed, however, even before 1938, in the course of sampling, that the *Molinia* in particular appeared to be slightly taller in the cages than in the controls. Actual observations showed that the tussocks in the former tend to be larger, the spaces between being devoid of other plants but filled with large quantities of dead leaves, etc. The vole burrows had almost disappeared, and the uppermost layer of the humus was much more compact. The remains of small dead *Molinia* tussocks were also found in the spaces. On the other hand, in the controls the *Molinia* formed a very even covering of small tussocks with no very large spaces between.

In view of the apparent differences in the height of the *Molinia* a method was devised and first used in 1935 to endeavour to measure any differences in the effective lengths of the *Molinia* tillers (including the longest leaf). In each cage and control two lines were pegged out parallel to but between the ordinary sample lines. Rough pinch samples were then taken at 6 in. intervals, the total number being about 100 in each quadrat. Care was taken to break off as many tillers as possible right at the base, and all complete ones in each sample were measured from their base to the apex of the longest leaf, the length being taken to the nearest 0·5 in. Any broken tillers were rejected and other species ignored. The lengths of the tillers in each sample were averaged out to obtain an average "sample" (or "tussock") length. The average lengths of all the samples containing tillers were then again averaged and the mean length of all the samples obtained. The double averaging was adopted to avoid the upsetting effect of a large number of tillers being plucked from an exceptionally tall or short tussock, no exact size of sample being possible. The results obtained are set out in Table 12, § (*a*). It is much to be regretted that figures for the previous years are not available, since the vole density was high in each district in 1932 and 1933. The figures in § (*b*) of the table give the average number of tillers of *Molinia* per sample obtained in the ordinary pinch sampling. These figures can be considered as providing an idea of the relative density of the *Molinia* and the lateral size of the tussocks. Uniform samples taken from the centres of large tussocks will tend to contain more tillers than those from small and probably less vigorously growing tussocks. The tussock length and average tiller number taken in conjunction will consequently give an idea of the relative luxuriance of the *Molinia*.

The length measurements of the *Molinia* tillers have all been examined statistically by Mr P. H. Leslie in order to see if any of the differences observed between the cages and controls are significant. He has kindly supplied the following note from which it will be seen that the tiller measurements for each cage or control have been treated in two ways, first, when grouped together to give the average "tussock length" of each sample (as in Table 12), and, secondly, when considered as individuals irrespective of the samples in which they occur. The results obtained by this second method are shown in Table 13.

Statistical notes on Molinia *tiller measurements*[1] (see Tables 12 and 13). In order to see whether the observed differences in the height of *Molinia* were statistically significant, the following calculations were made. If there were no difference between the cages and the controls, we should expect that the individual differences for each year would be distributed about a mean value at zero. For the methods of testing this hypothesis reference may be made to Fisher (1938, Chap. v), "Student's" *t* test being used. Taking first Corris cage 1 and its control, there are the four differences of 4·70, 5·15, 4·42 and 4·71 in. The mean difference is $4{\cdot}745 \pm 0{\cdot}1508$ and $t = \frac{4{\cdot}745}{0{\cdot}1508} = 31{\cdot}46$. From the tables of the distribution of *t*, for three degrees of freedom, a value of 5·841 would be

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[1] These statistical notes are based on the measurements as expressed in inches, which was the original method of measurement in the field.

Table 12. (*a*) *Average length of* Molinia *tillers in cm. and inches for four* Molinia *cages and three controls at Newcastleton and Corris during the years* 1935–8. *The figures in brackets represent the number of samples containing tillers; the percentage difference is calculated on the figures for the cage in each case*

	1935		1936		1937		1938	
Quadrat	cm.	in.	cm.	in.	cm.	in.	cm.	in.
Corris 1	55·12	21·70 (46)	58·29	22·95 (60)	57·15	22·50 (47)	50·93	22·05 (41)
Corris 1, control	43·18	17·00 (67)	45·21	17·80 (65)	45·92	18·08 (65)	38·96	15·34 (68)
Difference	11·94	4·70	13·08	5·15	11·23	4·42	11·97	4·71
% difference	21·5		22·5		19·5		23·5	
Corris 2	57·28	22·55 (39)	55·68	21·92 (45)	46·86	18·45 (47)	41·25	16·24 (50)
Corris 2, control	46·69	18·38 (45)	51·08	20·11 (45)	42·57	16·76 (31)	37·59	14·80 (37)
Difference	10·59	4·17	4·60	1·81	4·29	1·69	3·66	1·44
% difference	18·5		8·5		9		9	
Newcastleton 1	—		55·70	21·93 (41)	68·71	27·05 (41)	54·04	21·67 (38)
Newcastleton 3	—		54·05	21·28 (53)	65·18	25·66 (48)	51·46	20·26 (43)
Newcastleton, control	—		49·28	19·40 (60)	54·02	21·66 (53)	29·11	11·46 (45)
Difference, 1 – control	—		6·42	2·53	14·69	5·39	24·93	10·21
% difference	—		11·5		19·5		47	
Difference, 3 – control	—		4·77	1·88	11·16	4·00	22·35	8·80
% difference	—		9		15·5		43·5	

(*b*) *Average number of tillers per sample in same cages and controls during* 1936–8. *The figures in brackets represent the number of samples containing* Molinia; *the percentage difference is calculated as in* (*a*)

Quadrat	1936	1937	1938
Corris 1	4·45 (105)	3·44 (87)	4·99 (85)
Corris 1, control	3·38 (130)	2·84 (109)	2·84 (91)
Difference	1·08	0·60	2·15
% difference	24·5	17·5	43
Corris 2	4·14 (90)	3·40 (62)	3·44 (66)
Corris 2, control	3·74 (54)	2·67 (36)	3·30 (40)
Difference	0·40	0·73	0·14
% difference	9·5	21·5	4
Newcastleton 1	2·87 (86)	3·37 (79)	3·60 (78)
Newcastleton 3	2·28 (80)	2·64 (78)	2·58 (84)
Newcastleton, control	2·76 (86)	2·56 (75)	2·62 (60)
Difference, 1 – control	0·11	0·81	0·98
% difference	4	24	27
Difference, 3 – control	–0·48	0·08	–0·04
% difference	–21	3	–1·5

Table 13. *Average length of* Molinia *tillers in cm. and inches, for the same cages and controls as in Table* 12, *during the years* 1935–9, *taking the grand mean of all the tillers measured in each quadrat*

	1935		1936		1937		1938		1939	
Quadrat	cm.	in.	cm.	in.	cm.	in.	cm.	in.	cm.	in.
Corris 1	55·18	21·724	59·08	23·259	56·30	22·166	52·07	20·500	—	
Corris 1, control	42·49	16·729	44·98	17·710	46·72	18·392	38·56	15·183	—	
Difference	12·69	4·995	14·10	5·549	9·58	3·774	13·51	5·317	—	
Corris 2	58·35	22·971	54·03	21·273	46·82	18·439	40·44	15·922	38·85	15·295
Corris 2, control	46·69	18·380	53·50	21·064	46·93	18·476	38·44	15·134	43·04	16·945
Difference	11·66	4·591	0·53	0·209	–0·11	–0·037	2·00	0·788	–4·19	–1·650
Newcastleton 1	—		58·99	23·223	69·49	27·357	57·76	22·741	63·01	24·809
Newcastleton 3	—		55·75	21·950	66·40	26·143	53·44	21·039	—	
Newcastleton, control	—		49·96	19·679	57·22	22·529	31·64	12·455	31·47	12·389
Difference, 1 – control	—		9·03	3·544	12·27	4·828	26·12	10·286	31·54	12·420
Difference, 3 – control	—		5·79	2·271	9·18	3·614	21·80	8·584	—	

exceeded by chance in only 1·0 % of such random samples. There is thus little doubt that the observed mean difference of 4·745 is significantly different from zero. In the case of cage 2 and its control, the mean difference is 2·2775 ± 0·6355 in.: $t = 3{\cdot}58$, and for three degrees of freedom a value of 3·182 would be exceeded by chance in 5 % of such samples. Thus, if we adopt the customary level of significance of P, the probability of falling outside the range $\pm t$, equal to 0·05, the observed difference between the cage and its control must be regarded as just significant. Such borderline cases, however, must be interpreted with a certain amount of discretion. In adopting a level of significance of 0·05, 5 % of such cases will be regarded as real differences, when actually they may be due to random errors.

Turning to Newcastleton, there is first of all the comparison between cages 1 and 3, the differences for the three years being 0·65, 1·39 and 1·41 in. The mean difference is 1·15 ± 0·2501; $t = 4{\cdot}59$ and for two degrees of freedom $P = < 0{\cdot}05, > 0{\cdot}02$, and thus the difference between these cages is just significant. For the comparison between these cages and the control, there are two series of differences:

	Cage 1 − control	Cage 3 − control
1936	2·53	1·88
1937	5·39	4·00
1938	10·21	8·80

It will be noticed that in each case there appears to be a definite trend, the differences approximately doubling themselves each year. That is to say, that if y be the difference in any one year between the cage and control,

$$\log_{10} y = a + bt,$$

where t is time. The logarithms of the two sets of differences were taken and the values of b together with their standard errors were calculated by the methods described by Fisher (1938, Chap. v), the t test again being used to see whether the values of b are significantly different from zero. For cage 1 − control column $b = 0{\cdot}30295 \pm 0{\cdot}01472$, $t = 20{\cdot}57$, and for one degree of freedom $P = < 0{\cdot}05, > 0{\cdot}02$. For cage 3 − control, $b = 0{\cdot}33515 \pm 0{\cdot}003857$, $t = 86{\cdot}9$ and $P = < 0{\cdot}01$. Thus in both these cases the trend must be judged as being significant, the difference between the control and the cages being approximately doubled each year ($\log_{10} 2 = 0{\cdot}3010$). There appears to be no significant difference between the cages in this respect, since the difference between the two values of b is 0·0322 ± 0·01522, $t = 2{\cdot}11$, and for two degrees of freedom such a value of t would be exceeded in between 10–20 % of such random samples.

There is one further point. It is stated in the text that cage 1 at Corris consisted of *Molinia* as a dominant, while cage 2 was a mixture of two dominants, *Molinia* and *Deschampsia flexuosa*. Taking the four differences between the cages, we have −0·85, 1·03, 4·05 and 3·81. During the four years it appears that while the height of *Molinia* in cage 1 remained more or less constant, apart from yearly fluctuations, that of cage 2 became progressively lower. In order to test whether this trend was significant, a straight regression line was fitted to the differences ($d = a + bt$, time being the independent variable). The value of b was $1{\cdot}7 \pm 0{\cdot}4573$, whence $t = 3{\cdot}72$, and for two degrees of freedom $P = < 0{\cdot}1, > 0{\cdot}05$. Thus it is impossible to say from this data whether cage 2 was in fact becoming progressively lower as compared with cage 1.

The above calculations have been made under the assumption that the method of sampling was adequate and that the mean length in the pinches is a satisfactory estimate of the mean height of the *Molinia*. The number of measurements per pinch varied considerably. Another possible estimate is to take the grand mean of all the leaves measured and assume that the number per pinch will be related to the density of *Molinia* at the point sampled. Table 12 then reads as above (see Table 13), one further year being added, which has the advantage of giving one extra degree of freedom in testing the significance of the differences at Newcastleton. The results, using the same methods as above, are as follows. The mean difference between Corris cage 1 and control is $4{\cdot}9087 \pm 0{\cdot}3949$ and is definitely significant. Between cage 2 and the control the mean difference is $0{\cdot}7802 \pm 1{\cdot}0349$ and is not significantly different from zero. There is a significant difference between cages 1 and 3 at Newcastleton, the mean being $1{\cdot}3963 \pm 0{\cdot}1538$. Taking the four differences between Newcastleton cage 1 and control and fitting to them a straight regression line, $a + bt$, the value of b is $3{\cdot}209 \pm 0{\cdot}547$, $t = 5{\cdot}86$, and for two degrees of freedom P lies between 0·05 and 0·02. The trend is just significant. No significant trend could be determined with cage 3, but we have the results for only three years, and if a straight line be fitted to the logarithms of the differences, as was done before, $b = 0{\cdot}28875 \pm 0{\cdot}05023$, which for one degree of freedom cannot be regarded as significantly different from zero. Returning to Corris, the differences between cages 1 and 2 are −1·247, 1·986, 3·727 and 4·578; the value of b for the straight regression line is $1{\cdot}922 \pm 0{\cdot}379$, which just shows a significant difference from zero.

To summarize briefly: In both the series of mean values, Corris cage 1 is significantly greater than the control. In the case of cage 2 it is difficult to say whether the cage was higher than the control, and one cannot eliminate the possibility that cage 2 showed a definite trend downwards as compared with cage 1. At Newcastleton there appeared to be a definite difference between the two cages and, in the case of cage 1 at any rate, the differences between it and the control showed a significant yearly trend of approximately 3 in. a year.

It can be seen that on the basis of the figures in both Tables 12 and 13 the *Molinia* in most of the cages was more luxuriant than in the corresponding controls. At Newcastleton the lower figures for cage 3 than for cage 1, which are shown to be significant, are probably explained by the fact that the trees around cage 3 were on an average taller and in a much healthier condition than those around cage 1. The difference between cage 1 at Corris and its control was significant and remained approximately constant throughout the experiment. This may have been due to initial differences in the *Molinia* on the two areas, but it is also in agreement with the relatively constant vole abundance at Corris during that period. I am unable to suggest why the difference between cage 2 at Corris and its control is so much greater in 1935 than in subsequent years, but it may have some connexion with the successional changes dealt with more fully on p. 44. In any case the statistical treatment shows that the differences between this cage and its control for the whole period are not significant. At Newcastleton between 1936 and 1938 there has been a progressive increase in the difference between the cages and control, which is shown to be statistically significant for cage 1 at least, this corresponding with the increasing vole abundance which reached its maximum in the last year, particularly in the rides where the quadrats are placed. In 1938 in the control over 43 % of the tillers measured had the upper part cut off (almost certainly by voles), whereas in the cages the tips of all the leaves were normal. This biting off of the tillers obviously has an important effect in years of maximum vole attack, since frequently more than half of the lamina had been removed while sometimes only the stump of the tiller was left. Much the same vole effect was noticed in 1937 but no actual figures were obtained in that year.

In the *Holcus* quadrats density figures (corresponding to the tiller number values for *Molinia*) for 1936 were 1·96 in the cage to 2·05 in the control, and for 1937 1·81 and 2·08 respectively, differences which may fairly be considered as of no significance. Here again the tree effect must have been very great, and indeed was probably greater in the cage, around which the average heights of the trees in 1936 and 1937 were 74·3 and 93 in. respectively, whereas those around the control averaged only 62·4 and 75 in. in the corresponding years. In 1938 some voles gained access to the cage and completely demolished the vegetation; no sampling was done in this cage or its control.

It was not found possible to devise any satisfactory method of measuring tussock length or density in *Deschampsia caespitosa*. A selected number of the tallest inflorescences in the quadrats were measured each year with the results given in Table 14. Whether the difference between cage and control is significant cannot be ascertained with certainty from the data available, but it appears to be in agreement with the figures obtained for *Molinia*.

Table 14. *Heights of* Deschampsia caespitosa *inflorescences in cm. and inches*

Quadrat		1933	1934	1935	1936	1937
Cage 2	cm.	—	155–168	125–170	142–155	140–163
	in.	—	61–66	49–67	56–61	55–64
Control 2	cm.	119–153	122–153	—	119–142	130–155
	in.	47–60	48–60	—	47–56	51–61

(2) *The mosses*

The decrease of the mosses in all the cages has been so striking and uniform that it cannot be doubted that it is due to the enclosure of the caged areas. In no cage were there more than 15% of samples containing mosses by 1936, whereas in the controls the figures ranged from 25 to 90% of the samples. This is particularly well shown in the graphs (Fig. 4). Since the decrease occurs in areas free from voles there can be no question of any direct influence, and this is confirmed by field observations that voles practically never eat mosses. The effect must therefore be an indirect one, arising either from a change in soil or other altered conditions, or as a result of greater competition with other species. The figures for *Molinia* tussock length and density already given supply a partial explanation, since increase in these two factors inside the cage as compared with outside would result in increased shading of the mosses and, if continued, in their eventual death. Another factor, however, probably also enters here. The increase in the amount of leaf and other organic debris beneath the *Molinia* tussocks has already been mentioned. It is doubtful if the pleurocarpous mosses forming the chief moss vegetation can stand the continued burying and rotting effect of this accumulation. In most of the cages dead and dying remains of mosses could be found under this layer of debris. Only in the larger and more open gaps of the dominant grasses do the mosses survive, and then only in much decreased quantities.

In the controls, on the other hand, the mosses have maintained themselves during the experiments and at Newcastleton have even increased in quantity. It is evident that the action of the voles in keeping their runs clear will tend to prevent the accumulation of plant debris or at any rate will maintain it in a loose or disturbed condition which is favourable for the growth of mosses. The increase in the total amount of the mosses seems to be due almost entirely to proportional increases of the species already present, and though there are some signs of succession in the moss vegetation during the period of the experiment, this does not in itself account for the increase in abundance. Unfortunately, owing to our very scanty knowledge of the ecology, particularly the autecology, of bryophytes, it is scarcely possible to draw any conclusions from the changes in quantity of the various individual species.

It is interesting to note the effect in cage 2 at Newcastleton (*Deschampsia caespitosa* dominant) of the access of voles in 1937 following the corrosion and breaking of the wire at and just below ground level. Between 1932 and 1936 the percentage frequency figures of mosses had fallen from 57 to 7·5 (see Table 8), but after that it rose again to 27 in 1938 (see also Fig. 4). This seems mainly due to the decrease in the dominant, since the total figures for all other angiosperms also rose between 1936 and 1938 from 60 to about 90. Although there was a considerable tangle of various plants in the cage in 1938, the large masses of radiating dead tillers and leaves usually associated with *Deschampsia* had greatly diminished.

This recovery of the mosses in cage 2 following vole entry is of considerable importance since it shows that the decrease of the mosses in the cages was not due merely to the erection of wire around the areas concerned. It was thought possible that the wire might have reduced the clearing effect of wind and caused the accumulation of debris, thus choking the mosses. As, however, the recovery of the mosses mentioned above took place while the wire was still in position, the openings being only quite small ones, it is clear that in this cage at least the presence of wire was not in itself the cause of the striking decrease in the mosses up to 1937. It appears equally evident that the presence of voles is advantageous to the mosses.

(3) *Angiosperms, apart from the dominants*

It seems probable that the general decrease of non-dominants in cages 1, 3 and 4 at Newcastleton as compared with the maintenance of their abundance or smaller decreases in the controls is, as suggested for the mosses, a question of differential competition. Some of these species, e.g. *Juncus acutiflorus*, *Potentilla erecta*, *Scirpus caespitosus*, are eaten, or at least cut up, by voles, but this naturally could not take place in the cages. It therefore seems likely that the increase in the dominants in the cages as a result of the removal of vole attack has an unfavourable effect on other species, these latter tending to be crowded or shaded out. It is interesting to note that in the *Deschampsia* cage at Newcastleton the non-dominant angiosperms have increased. *D. caespitosa*, however, does not form such a close stand as either *Molinia* or *Holcus*, there being considerable spaces between the tussocks, in which other species occur. Consequently the removal of vole attack and presumed resulting increase in luxuriance of the *Deschampsia* do not affect adversely these other species as in the cages occupied by the closer growing dominant grasses. Indeed the other species probably benefited themselves by the absence of direct vole attack. With the invasion of this cage by voles in 1937 and accompanying marked decrease in the *Deschampsia* the other angiosperms have increased even more in total amount. Presumably the removal of nearly all competition with *Deschampsia* more than compensated for the return of the voles.

It is possible, however, that, as in the quadrats at Corris discussed below, the changes are partly successional ones taking place independently of vole action. Since the start of the experiment *Deschampsia* has decreased markedly on the slope bearing the quadrats, especially during the period 1936–9, and is apparently being replaced by a mixed vegetation of *Juncus* spp. and various grasses, especially *Holcus mollis*.

With regard to the decrease of non-dominant species in both controls at Corris, it is probable that we here are recording a normal succession from a mixed community to a purer *Molinia* community. It should be noticed that both cage 2 and its control were set down originally in *Molinia* with a strong admixture of *Deschampsia flexuosa*, this community occupying a comparatively small area and being possibly a remnant of what had been previously a more extensive community. The area included patches of *Eriophorum*, *Sphagnum*, *Calluna*, *Erica Tetralix*, *Empetrum*, etc., and was obviously very closely related to the type of bog moorland which occurs on less well-drained peat than does *Molinia*. Drainage of the area has been maintained since planting and as a result the vegetation has changed to a great extent into a *Molinia* community similar to that all around, of which characteristic portions were included in cage 1 and its control. The typical rather dwarf bog-moorland community has a distinctly irregular surface with alternating higher and lower parts, and this permits of the existence of a comparatively varied flora, the drier-loving components of which occupy the hummocks, while the more genuine bog species occur in the hollows. The advent of *Molinia* provides instead a tall dense relatively level-topped community in which only other equally tall species can flourish. The area of control 2, however, still includes a number of patches where there is little or no *Molinia*, and here the vegetation has maintained to a great extent its original character. The control to cage 1 probably represents a later stage in this succession than does control 2, but here also the phanerogams are steadily decreasing, the vegetation thus becoming more and more like that in cage 1 which is almost pure *Molinia*.

(4) *Fluctuations*

Fluctuations in the frequencies of all the species, dominant or otherwise, is evident on examination of the tables and graphs. The changes in the frequencies of the rarer species from year to year may be more apparent than real, since it is probable that the small differences in the tables are not necessarily significant owing to the manner in which the samples are taken. (The lines of samples are only approximately in the same positions in successive years.) On the other hand, the considerable changes shown by the dominants or by large species groups are well outside the limits of experimental error, and must therefore be due to some outside influence. Some of these major differences have not yet been interpreted, since there are not sufficient data for the purpose. Others, however, can be reasonably explained by comparison of known data, such, for instance, as the rainfall (see Table 15). One particularly dry growing season both at Newcastleton and Corris was 1933, and the graphs and tables show in many cases that the frequency figures for this year were lower than for 1932 and 1934. Observations at the time of our visit showed the ground to be relatively dry, this having been noted also by zoological investigators at visits earlier in the year. 1936 was another year with a dry growing season at Newcastleton and it will be seen that the frequency figures for most species and species groups are especially low for that year. As the dominants in particular are in most cases plants which prefer a rather moist habitat the dry growing season would affect them adversely. In addition, the high organic content of the soil reduces the available water and easily causes drought conditions to develop in the presence of the much improved drainage associated with planting.

Table 15. *Rainfall in inches during the months March–June and cm. (brackets) at Newcastleton and Machynlleth*

	1932	1933	1934	1935	1936	1937	1938
Newcastleton	13·90 (35·4)	10·14 (25·8)	15·26 (38·8)	11·37 (29·0)	8·93 (22·7)	11·19 (28·5)	13·53 (34·4)
Machynlleth	16·96 (43·2)	16·18 (41·2)	20·77 (52·8)	19·19 (48·8)		Not available	

7. GENERAL CONCLUSIONS

The experiments carried out during the period 1932–8 have shown that voles exert a definite influence on the vegetation in the two areas studied. The general effect is apparently that of reducing the luxuriance of the dominant grasses so that other flowering plants and especially mosses are enabled to exist more abundantly among the dominants. On removal of the vole attack the non-dominants, particularly the mosses, decrease in abundance, apparently as a result of the increased competition with the more luxuriant dominants. Voles therefore tend to preserve a relatively open vegetation, comparatively rich in species. This is presumably effected by the direct eating or cutting up of the aerial parts of the dominants, and by the complicated series of burrows below the main surface of the vegetation, the formation and maintenance of these burrows preventing the development of large tussocks of grasses like *Molinia* or of thick matted turf-like growth as in *Holcus mollis*.

Although these effects of the voles on the vegetation are easily demonstrable from the observations made and data collected, it has not always been easy to correlate the degree of vole effect with the fluctuations in the vole abundance in different years. Starting with a high vole abundance at Corris in 1932, the first year of the experiments, the abundance there has slowly declined in subsequent years so that it has been increasingly difficult to detect any direct relationship between vole abundance and the state of the vegetation at any given period.

At Newcastleton conditions have been more favourable. Here again the vole abundance was high in the first year or so of the experiments, dropped to a minimum in 1935 and 1936 and rose again to a second maximum in 1937 and 1938. The effect of the latter maximum has been mentioned before (pp. 26, 41) and was evident not only from field observations and superficial examination of the vegetation, but also in the decrease in the lengths of the *Molinia* tillers as revealed by actual measurements. The re-entry of the voles into one cage (cage 2) and the recovery of the mosses following this shows that some of the effects of vole exclusion are quite quickly reversed when the voles obtain access to the vegetation.

Two factors have tended to interfere with or mask any results obtained during the experiments. First, there is the general change in conditions following the exclusion of grazing animals and the formation of an extensive and effective drainage system. This has resulted in the extremely luxuriant growth of *Molinia* and *Deschampsia caespitosa* and the gradual disappearance of boggy areas dominated by *Eriophorum* and other similar species. At Corris, as has been shown already, this replacement of bog by *Molinia* is apparently still taking place in some of the experimental quadrats. Presumably this general succession is still progressing everywhere, although at Newcastleton it is difficult to say in what manner, line transects repeated at several years' intervals having revealed only a few obvious changes. The latest line-transect survey shows, for instance, that *Deschampsia caespitosa* decreased markedly between 1935 and 1939, while in the same period there was an increase in the abundance of species of *Juncus*, viz. *J. effusus*, *J. conglomeratus* and *J. acutiflorus*. The only change of this type which has been noted in the quadrats themselves has been the invasion of two of the cages (nos. 2 and 3) by *Holcus mollis*. This can be easily traced in the charts of the samples from year to year, and will be seen in the tabular summaries given earlier. The invasion in each case has taken place spatially from one side or corner of the cage by means of the characteristic runners of the species. There are signs in the line-transect charts that a similar spread of *Holcus* is taking place in many other localities, but it is from its very nature a slow process.

The other interfering factor is the growth of the planted trees, the effects of which have been discussed previously. It seems probable that the net effect of root competition and the actual drying effect on the soil tends towards the replacement of the deeply rooting and moisture-loving species by those which flourish in drier conditions. So far the direct action of shading, which is of course very considerable in dense evergreens like spruces, has evidently been of little importance except perhaps in the case of a few particularly tall trees. The figures for the majority of the Newcastleton quadrats, which lie in a narrow ride, indicate that the trees had already begun to exert their influence during 1936 and 1937 if not to any appreciable extent before. This has tended to obscure not only the vole effect, but also the general succession already mentioned.

A further series of quadrats was started in 1937 in an area at Newcastleton which had just been planted. This will enable at least one whole vole cycle to be followed during the early stages of succession following enclosure and drainage and before the trees have grown to any extent. It will also be possible to improve and add to the methods already used in the light of the results obtained during the first series.

8. SUMMARY

1. An account is given of experiments carried out in conjunction with the Bureau of Animal Population, Oxford University, to endeavour to ascertain the effects of the common field vole (*Microtus agrestis*) on vegetation.

2. Two localities were selected for the experiments, namely, the Newcastleton State Forest, Roxburghshire, Scotland, and the Corris State Forest, Merionethshire, Wales, both by kind permission of the Forestry Commission. The trees surrounding the experimental quadrats were from 3 to 6 years old when the work began in 1932.

3. Selected areas in the rides between the trees were fenced round with fine mesh wire 4 ft. 6 in. in height and sunk 1 ft. 6 in. in the earth (the cages). Controls, consisting of similar areas but without the wire, were also marked out. These quadrats were placed mainly in communities of *Molinia caerulea* but at Newcastleton also in those of *Deschampsia caespitosa* and *Holcus mollis*.

4. By means of a method of "pinch" sampling an analysis of the vegetation in the cages and controls was made annually from 1932 to 1939, during which period members of the Bureau carried out six-monthly estimates of the vole abundance over the area in which the quadrats were established.

5. The most definite results of enclosure were the decrease of angiosperms other than the dominants in many of the cages and the almost total disappearance of mosses in all the cages. This is probably due to an increase in vigour of the dominant species following the removal of vole attack, and the consequent increase in competition between the dominants and the subordinate species. The presence of voles with their feeding and tunnelling activities tends to keep the community more open and thus to create a habitat favourable to the continued existence of a greater number of species.

6. In order to assess more accurately the effect of voles on *Molinia* numerous measurements were made. These show that, at any rate at the time of maximum vole abundance, the lengths of the tillers are considerably greater in the cages than in the corresponding controls. This is due partly to actual biting off of the ends of the tillers, and partly to the weakening of the plants following general burrowing and nibbling activities.

7. The gradual succession following enclosure and drainage tends to mask the effects caused by the voles, as also does the growth of the planted trees. The influence of the former is probably more evident at Corris, that of the latter more obvious at Newcastleton.

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THE EFFECT OF MANURING, GRAZING AND CUTTING ON THE YIELD, BOTANICAL AND CHEMICAL COMPOSITION OF NATURAL HILL PASTURES

II. CHEMICAL SECTION

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(*With one Figure in the Text*)

As indicated in the previous number of this *Journal* (**1**), this experiment on natural hill pastures involved a combination of two treatments, namely intensive manuring and controlled grazing. The effect on the herbage has been unique in that this combination produced a change known to be impossible by either treatment alone, and only accomplished previously on the poorer areas with the assistance of the cultivator and the sowing of seed. The herbage modifications following the manuring and grazing are shown in the Yield and Botanical Section to have increased in importance with the progress of time. When the experiment had reached its ninth year, the sward transformations were of such significance that it was considered desirable during the tenth growing season to examine both the herbage and the soil in the various plots so as to determine some of the more important chemical changes effected in each by the different treatments.

Although the three centres chosen for the experiment represent hill land of similar altitude they differ greatly in soil conditions, and are typical of the wide fluctuations in the soil of the sheep walks of this part of the country. The Llety-*Molinia* soil represents the most acid type in the area. In it there is a large accumulation of organic matter and defective drainage, while the leaching of minerals has led to extreme poverty in essential constituents. Leaching has also been active at the Llety-fescue and Bwlchrosser centres, but the soils here have not the extreme acidity of that at the Llety-*Molinia* centre, and conditions in them are drier than in the *Molinia* soil.

EFFECT OF TREATMENT ON THE CHEMICAL COMPOSITION OF THE HERBAGE

Table 1 indicates the effect of the various treatments detailed in the previous issue of this *Journal* (**1**) on the chemical composition of the herbage cuts taken in 1939 at Bwlchrosser. These figures have been obtained by taking the average for the several cuts obtained in the growing season, and are expressed as percentages of the dry matter.

In spite of the much greater growth on the manured plots compared with that on the control, the manurial dressings have brought about a significant increase in the protein concentration of the PKN and P plots, while the concentration has not been significantly changed in the CaPKN and Ca plots. It is seen that in all cases the manured plots gave a less fibrous herbage than the control.

Table 1. *Chemical composition of herbage from enclosed plots at Bwlchrosser centre*

Average values for 1939 cuts expressed as percentage of dry matter

Plot	% protein	% crude fibre	% lime (CaO)	% potash (K_2O)	% phosphate (P_2O_5)
Pasture CaPKN	12·81	22·15	0·939	3·71	0·744
„ PKN	13·44	21·50	0·595	3·55	0·730
„ Ca	12·37	21·30	0·959	3·19	0·451
„ P	13·64	21·00	0·917	3·45	0·772
„ control	12·69	24·30	0·633	2·81	0·361

When the concentration of lime in the herbage is considered, the control plot and the PKN plot stand out in marked contrast to the other three plots in which the lime content is at a much higher level. It is evident that clover is the most important determining factor where the calcium of the herbage is in question. The control plot and the PKN plots contained only traces of clover, while the percentage of clover in the other three plots ranged from 14 to 22 %.

The concentration of potash has been increased in the produce of all treated plots compared with the control, the greatest effect in this respect being obtained in the CaPKN plot.

In so far as chemical composition is concerned, the greatest effect of the treatments at Bwlchrosser has been on the phosphate concentration of the herbage. The inclusion of superphosphate in the manurial dressings has invariably resulted in more than doubling the concentration of herbage phosphate. The phosphate concentration has, in fact, been changed from what is typical of upland pastures to what is representative of a large proportion of lowland herbage (**2**).

Table 2 shows the effect of the different treatments on the concentration of constituents in the herbage from the Llety-fescue centre.

Whereas the effect of calcium with and without manures was insignificant on the protein of the Bwlchrosser herbage, its effect has been marked on the protein in the Llety-fescue sward. Calcium alone has raised the protein concentration by 18 %, while calcium in conjunction with complete manures has raised it by 26 %. In this connexion it is of interest to note that while at Bwlchrosser the bent-fescue ratio was lowered as a result of applying calcium with and without manures, at Llety-fescue the calcium had the extreme opposite effect in that it practically eliminated the fescue in favour of bent. In addition the influence of the calcium on the wild white clover content of the herbage was greater at Llety-fescue than at Bwlchrosser, the wild white clover in the Ca plot at Llety-fescue being 19·5% compared with 14·6% at Bwlchrosser, and being 27·3% in the Llety-fescue CaPKN plot compared with 14·3% at Bwlchrosser.

Table 2. *Chemical composition of herbage from enclosed plots at Llety-fescue centre*

Average values for 1939 cuts expressed as percentage of dry matter

Plot	% protein	% crude fibre	% lime (CaO)	% potash (K_2O)	% phosphate (P_2O_5)
Pasture CaPKN	15·75	23·71	1·099	3·40	0·786
,, PKN	14·00	25·78	0·514	3·28	0·783
,, Ca	14·75	23·73	0·868	2·95	0·580
,, P	13·94	25·01	0·724	2·99	0·846
,, control	12·50	25·00	0·486	2·31	0·376
Hay CaPKN	14·38	25·18	0·661	3·20	0·739
Hay control	12·75	26·30	0·483	2·44	0·441

The effect of the P and PKN on the protein has been similar to that effected by these manures at Bwlchrosser.

A comparison of the protein of the hay plots with that of the pasture plots shows that the grazing animal only influences the herbage favourably under conditions of liberal manuring. While the sheep has had no significant effect on the herbage protein of the control plots, it has raised the protein concentration of the completely manured plot.

At this centre only the manurial treatments that included calcium were successful in reducing the fibre content of the sward.

The effect of the various treatments on the lime, potash and phosphate of the herbage shows the same general tendencies as at the Bwlchrosser centre, there being one important difference, viz. that the influence of CaPKN on the lime has been far greater here than at Bwlchrosser. Although the concentration of lime in the control plots at Bwlchrosser is decidedly greater than at Llety-fescue, the concentration of the same constituent in the CaPKN plots is decidedly greater at Llety-fescue than at Bwlchrosser. As a consequence while lime with complete manures has increased the pasture lime by 48% at Bwlchrosser, it has increased it by 126% at the Llety-fescue centre. This is largely explained by the fact that wild white clover established itself much more successfully on the CaPKN Llety-fescue plot than on the similarly manured plot at Bwlchrosser.

It is evident that the outstanding concentration of lime in the CaPKN herbage has not been attained through the mere application of manures, but that controlled grazing has been a most important contributory factor. The application of the same manures without the grazing animal raised the herbage lime by 37%, but when the animal entered the scene it was raised by

126 %. On the other hand, without the application of the manures the animal did nothing whatsoever to the lime content of the sward.

Table 3 gives the influence of the various treatments on the composition of the herbage from the Llety-*Molinia* centre.

Table 3. *Chemical composition of herbage from enclosed plots at Llety-*Molinia *centre*

Average values for 1939 cuts expressed as percentage of dry matter

Plot	% protein	% crude fibre	% lime (CaO)	% potash (K_2O)	% phosphate (P_2O_5)
Pasture CaPKN	16·75	23·08	1·155	4·00	0·887
„ PKN	13·81	27·66	0·574	3·31	0·811
„ Ca	17·12	23·45	1·185	3·06	0·558
„ P	12·43	26·96	0·549	2·65	0·834
„ control	11·19	28·71	0·418	1·63	0·276
Hay CaPKN	12·45	30·21	0·560	2·09	0·525
Hay control	9·84	26·93	0·363	1·18	0·241

As seen from the above table the effects of the treatments on the *Molinia* area differ in several important respects from their effects at the other two centres. A comparison of the hay control and the pasture control shows that the animal itself in the absence of artificial manures has influenced the herbage in that the concentration of protein and mineral matter has been raised. This coincides with the fact that the pasture control contained less *Molinia* and more bent than the hay control.

The influence of the animal alone is, however, small compared with its influence in conjunction with manures. This joint influence has been far more pronounced at this centre than at the others. The maximum increase effected on the protein at the other centres amounted to 26 % compared with an increase of 53 % on the Ca plots at this centre. The effect on the lime of the herbage has also been much greater here than elsewhere, an increase of 184 % in lime concentration following the application of lime alone, the effect of lime with complete fertilizers being only slightly less than this. A greater effect has also been produced on the concentration of plant potash, particularly as a result of applying lime and complete manures. The greatest change of all has, however, been produced in the phosphate content of the herbage, the increase in this on the CaPKN plot compared with the control being 221 %.

As at Llety-fescue those manurial treatments that included calcium have been most effective in reducing the fibre content of the pasture. While calcium with complete manures has been effective in reducing fibre in the pasture plots, it has not produced this effect on the hay plots.

EFFECT OF TREATMENT ON THE YIELD OF CHEMICAL CONSTITUENTS

Owing to the influence of these different treatments on the concentration of the herbage ingredients and also their effect on the productivity of the sward, far-reaching changes in the yield of nutrients have occurred at the different centres. The yields of protein, lime and phosphate from the control and treated plots at the three centres are given in Table 4.

Table 4. *Total yields of nitrogen, lime and phosphate from enclosed plots during* 1939 *at* (1) *Bwlchrosser;* (2) *Llety-fescue;* (3) *Llety*-Molinia

Yield in lb. per plot

	Nitrogen			Lime (CaO)			Phosphate (P_2O_5)		
Plot	1	2	3	1	2	3	1	2	3
Pasture CaPKN	1·110	1·541	1·598	0·537	0·670	0·754	0·424	0·496	0·553
,, PKN	0·944	0·948	1·074	0·257	0·210	0·269	0·315	0·343	0·405
,, Ca	0·784	1·048	1·175	0·384	0·372	0·511	0·185	0·261	0·232
,, P	0·790	0·891	0·500	0·322	0·284	0·142	0·278	0·332	0·197
,, control	0·231	0·316	0·167	0·071	0·077	0·044	0·040	0·056	0·024
Hay CaPKN	—	0·713	0·229	—	0·215	0·065	—	0·233	0·060
Hay control	—	0·267	0·095	—	0·082	0·026	—	0·058	0·015

From the above it can be concluded that the inclusion of lime in the manurial dressing has a profound effect on the yield of herbage nitrogen at both Llety centres, but that the influence of lime on nitrogen yield is less at Bwlchrosser. The lowest yield of pasture protein is obtained from the *Molinia* control plot, while the highest yield is obtained from the plot receiving lime and complete fertilizer at the same centre. This is not only true regarding the protein, but also regarding the lime and the phosphate yield.

The potential value of the *Molinia* area is, therefore, very high for the production of pasture protein, being somewhat greater than the fescue area and much greater than the Bwlchrosser area. Its potential value for the production of hay protein is, however, small and markedly inferior to that of the fescue centre.

In Fig. 1 A the effect of the treatments on the nitrogen yields from each pasture cut is shown, the yield from each cut in the control plot being taken as 100. This comparison indicates that the most effective treatment in raising the nitrogen yield at all centres has been the application of lime with complete manures (CaPKN plot). This application has produced its maximum effect at Bwlchrosser and at Llety-fescue in the May cut, when, for every 100 lb. of nitrogen yielded by the control plot, 1619 lb. were yielded by the CaPKN plot at Bwlchrosser and 1955 lb. by the similarly treated plot at Llety-fescue. On the other hand, the maximum yield from this treatment at Llety-*Molinia* was obtained in the September cut, and for every 100 lb. of nitrogen derived at this time from the control plot, 1925 lb. were yielded by the CaPKN plot.

The curves for the calcium carbonate treated plot (Ca plot) show that while the effect of calcium in raising the protein yield has been very significant at all centres, it has been much greater on the *Molinia* soil than on the less acid soils at the other two centres. The PKN treatment has also been more effective in raising the yield from the first three cuts at the *Molinia* centre than at either of the other two.

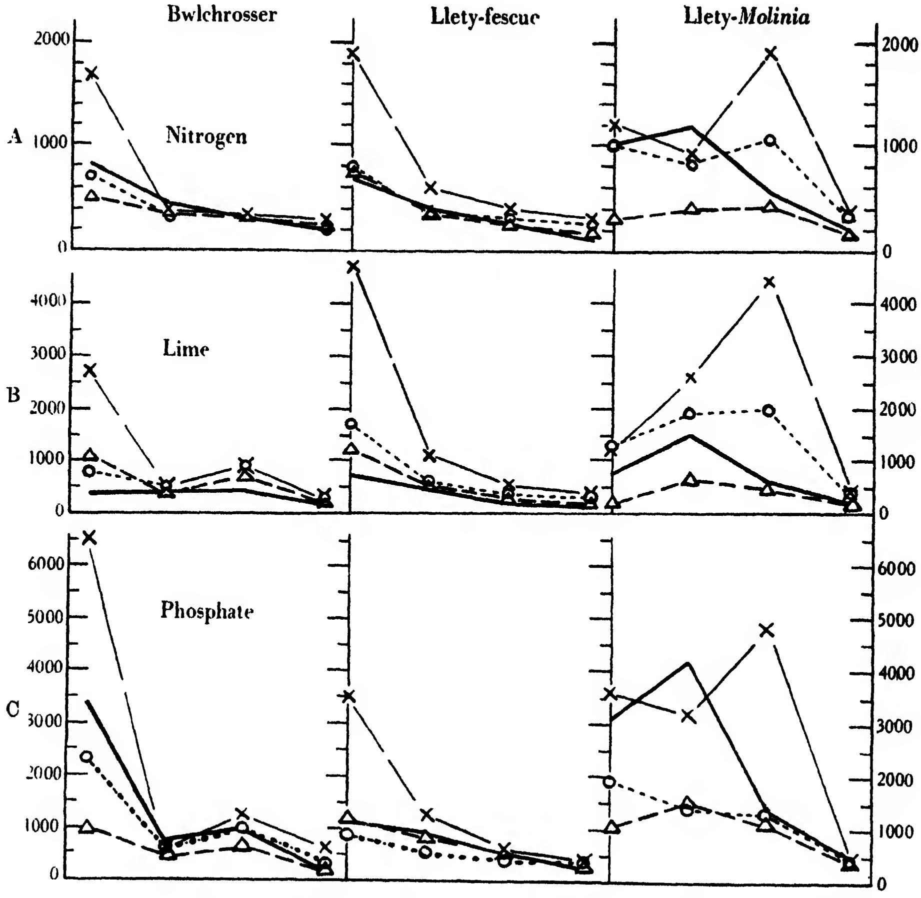

Fig. 1. Effects of different treatments on yields of A, nitrogen, B, lime (as CaO) and C, phosphate (as P_2O_5) at the three experimental localities. The yields are given as percentages, the control plot yield being taken as 100. The four cropping dates (horizontal scale) were 22 May, 14 July, 5 September and 30 October. Plot symbols: CaPKN X——, PKN ——, Ca o - - - -, P △——.

Phosphate (in the form of superphosphate) as a single factor in influencing protein yield is seen to be of greater importance than calcium at Bwlchrosser, for not only has it led to the contribution of more total protein in the herbage cuts when taken together, but it has also made a greater contribution towards earlier protein supply. At Llety-fescue, on the other hand, the calcium has given a slightly greater yield of both early and late protein, as well as a somewhat greater total supply of protein for the season. At Llety-*Molinia* the superiority of lime over superphosphate as a single factor influencing protein productively is unmistakable, there being much greater yields throughout the season from the application of lime than from the application of superphosphate.

When potassium and nitrogen are added to the phosphate (PKN plots), the effect at Bwlchrosser while definite is not large and is confined exclusively to the first two cuts. The addition of these two same elements to the phosphate at Llety-fescue has had no significant effect in raising the protein yield. At Llety-*Molinia* these two elements have contributed towards a much greater yield, particularly in the first two cuts, than that obtained from phosphate treatment only. It is of interest to note, however, that at Llety-*Molinia* the lime treatment by itself has been as effective as the PKN treatment in so far as total protein productivity is concerned, the difference being that the PKN plot has supplied the protein earlier in the season than the Ca plot.

The effect of the different treatments on the lime (CaO) yield (Fig. 1 B) follows the same general lines as their effect on the protein. It should be emphasized, however, that the effect of these treatments on the lime is of a different order to their effect on protein yield. Thus when the control plot is taken as supplying 100 lb. of protein, the maximum yield of protein following treatment amounts to 1955 lb., while the maximum single cut yield of lime for every 100 parts produced on the control plot amounts to 4625 lb. as a result of treatment.

At Bwlchrosser and Llety-fescue the effect of calcium carbonate application alone (Ca plot) is similar to that of the superphosphate application by itself (P plot). On the other hand, the herbage lime yield at Llety-*Molinia* has been influenced to a much greater degree by the limestone dressing than by the superphosphate application. The addition of potash and nitrogen to the phosphate has slightly depressed the yield of lime at Bwlchrosser and Llety-fescue, but has decidedly increased it at Llety-*Molinia*. Calcium carbonate alone has been more effective in increasing the pasture lime yield at all centres than has been the joint application of phosphate, potash and nitrogen.

The outstanding fact in connexion with the effect of the treatments on phosphate yield (Fig. 1 C) has again been the profound influence of the CaPKN treatment. For example, in the first cut at Bwlchrosser, for every 100 lb. of phosphate supplied by the control plot, 6550 lb. have been yielded by the CaPKN plot. All the treatments are found to have had a greater effect on the phosphate yield of the first cut at Bwlchrosser than on the lime yield (Fig. 1 B) from the same cut at this centre.

At Bwlchrosser phosphate as a single fertilizing factor is seen to have a decidedly greater influence on phosphate productivity than lime. At Llety-fescue the difference between the lime and phosphate plots is less, while at Llety-*Molinia* the influence of lime is slightly greater than that of phosphate in its contribution towards herbage phosphate. At the latter centre not only has the lime given a greater total phosphate productivity, but it has also led to a superior yield of sward phosphate at the commencement of the growing season.

EFFECT OF THE PASTURE TREATMENT ON THE SOIL AT THE THREE CENTRES

Samples of soil from the experimental plots were taken in April, July and November of 1939, and the change effected by the treatments on the soil *p*H and exchangeable lime is indicated in Table 5.

Table 5. *Effect of treatments on the* pH *and the exchangeable lime of the soil at the three centres:* (1) *Bwlchrosser;* (2) *Llety-fescue;* (3) *Llety*-Molinia

	*p*H			% exchangeable lime (CaO)		
Plot	1	2	3	1	2	3
Pasture CaPKN	6·02	5·51	4·98	0·140	0·154	0·151
„ PKN	4·63	4·33	3·82	0·041	0·026	0·023
„ Ca	5·97	6·12	5·23	0·170	0·212	0·159
„ P	4·96	4·70	4·09	0·042	0·033	0·037
„ control	4·80	4·53	3·99	0·031	0·014	0·008

Table 5 shows that the effect of the superphosphate and also that of superphosphate plus potassic and nitrogenous fertilizers has been very small on the *p*H of the soil. The tendency at the three centres has been for the superphosphate slightly to decrease the acidity, while the three combined fertilizers have slightly increased it, this latter effect being doubtless mainly due to the sulphate of ammonia. In contrast to the small influence of the fertilizers, the effect of the limestone in diminishing the acidity has been profound at all three centres. This is true both where the limestone was applied alone and where applied in conjunction with the complete fertilizers, the influence of the limestone alone being somewhat greater than that of the lime plus fertilizers at the two Llety centres.

The applications of 2 tons of limestone in 1930 and 1935 effected a marked improvement in the lime status of the soil as shown by the increase in exchangeable lime. A mean value of 0·018% exchangeable lime in the control plots has been increased to 0·180% in the Ca plots. This means that the average annual loss of lime from the soil of the Ca plots amounted to 139 lb., 36 lb. of this finding its way into the herbage and 103 lb. being lost through leaching. The average annual loss from the soil of the CaPKN plots amounted to 211 lb., 59 lb. of this being returned in the herbage and 152 lb. lost through leaching. When the high rainfall at these centres is taken into consideration, it is seen that the ratio between the lime recovered in the herbage and that leached is exceptionally high both on the Ca and on the CaPKN plots. The grazing animal has been an important factor in contributing towards this high ratio. This is borne out by the fact that in the CaPKN hay plots the total average annual loss of lime has amounted to 217 lb., while only 9 lb. out of this total has been recovered in the hay.

The next table gives the effect of the treatments on the available potash and phosphate in the soil.

Table 6. *Effect of treatments on available potash and phosphate in the soil at the three centres:* (1) *Bwlchrosser;* (2) *Llety-fescue;* (3) *Llety*-Molinia

	% available potash (K_2O)			% available phosphate (P_2O_5)		
Plot	1	2	3	1	2	3
Pasture CaPKN	0·035	0·033	0·034	0·016	0·017	0·015
„ PKN	0·032	0·027	0·039	0·015	0·012	0·011
„ Ca	0·022	0·025	0·031	0·003	0·004	0·008
„ P	0·019	0·019	0·034	0·013	0·013	0·012
„ control	0·026	0·021	0·030	0·003	0·004	0·005

From the above it is seen that the application of potash salts has had the effect of raising the available potash in the soils of the three centres. The influence of potash application has, however, been far more outstanding in the composition of the sward than in that of the soil, and this experiment indicates that most of the potash added to the soil has been quickly absorbed by the herbage. Due to this it is found that in the CaPKN plots the mean increased yield of herbage potash compared with the control plots has been as follows over the season under investigation (lb. per acre K_2O):

Bwlchrosser	Llety-fescue	Llety-*Molinia*
178	175	226

This large increase much more than fully accounts for the seasonal application of potash, which amounted to 120 lb.

On the other hand, the conditions are found to be very different in the absence of the grazing animal on the hay plots. Here the mean annual increment of potash in the hay of the CaPKN plots amounted to 42 lb. in excess of the control. The remaining potash is accounted for in the soil, a high proportion of it being in an available form, there being 0·033% available potash in the CaPKN hay plots compared with 0·024% in the hay control plots.

While the soils of the control plots contain a good supply of available potash, Table 6 shows that the available phosphate in these soils is decidedly low, and that the application of phosphate has brought this to a more satisfactory level. Except at Llety-*Molinia* the application of limestone has effected no increase in the amount of readily available phosphate. In spite of this, limestone has led to a much greater yield of herbage phosphate compared with the control plots (Table 4), and this is probably due to the important effect of calcium on the root system in these lime-deficient soils. It is also possible that, although the lime has not increased the proportion of readily available phosphate, it may have increased the concentration of soil phosphorus which the herbage can slowly utilize.

SUMMARY AND CONCLUSIONS

The changes produced by intensive manuring and controlled grazing on the chemical composition of the following pasture types are given.

1. An enclosed hill *Festuca-Agrostis* association. Here the untreated sward was typical in protein and phosphate of the enclosed upland grazings in Mid-Wales, but showed a lime content higher than the average for such swards.
2. An open hill *Festuca-Agrostis* association. The untreated sward in this area was similar in protein and phosphate concentration to the former, but showed a lower lime content.
3. An open hill *Molinia* association. Here the untreated herbage was the lowest in protein, lime and phosphate concentration, its content of these nutrients showing it to be representative of the poorest type of herbage to be found in the sheep walks of the area.

These three types were similarly subjected to a number of manurial treatments and controlled grazing by sheep. The manurial treatments included the application of limestone alone, and limestone in conjunction with liberal applications of fertilizers (viz. superphosphate, potash salts, sulphate of ammonia).

As a result of these treatments a much higher concentration of nutrients was derived from all three types of pasture. The greatest effect of the treatments on the enclosed *Festuca-Agrostis* association was found in the increase in phosphate concentration of the herbage, this being changed from what is typical of upland pastures to what is representative of a large proportion of lowland herbage.

In the open hill *Festuca-Agrostis* area the manurial treatments that included limestone were very effective in raising the protein concentration of the herbage. They were also outstanding in their effect on the lime content of the sward. While limestone with complete fertilizers increased the pasture lime concentration by 48 % in the enclosed hill *Festuca-Agrostis*, the same treatment increased the pasture lime concentration by 126 % in the open hill *Festuca-Agrostis* area. In the latter area the effect of the controlled grazing on the chemical composition was clearly brought out. It is shown that one influence of the sheep was to raise the protein concentration of the herbage from those plots receiving limestone and complete fertilizer. While the application of lime and complete fertilizer without grazing raised the herbage lime by 37%, the introduction of the grazing animal raised the lime concentration by 126%.

The effect of the grazing animal in conjunction with manures was far more pronounced at the *Molinia* centre than at either of the other two centres. The herbage was changed in composition to such an extent that instead of being representative of the poorest type of hill grazing it excelled the herbage similarly treated at the two *Festuca-Agrostis* centres in protein, lime, phosphate and potash concentration, and became of equal value to lowland types in nutrient content.

The far-reaching changes in the yield of nutrients that occurred at the three centres are shown. The lowest yields of nutrients were obtained from the untreated *Molinia* pasture, but the same pasture as a result of manuring and controlled grazing gave higher yields than those obtained from the other two pastures similarly treated.

The most effective treatment in raising the protein yield at all centres proved to be limestone in conjunction with complete fertilizer. Limestone alone was, however, very effective in raising the protein yield, its effect being greatest at the *Molinia* centre where the soil conditions were most acid.

Superphosphate alone was more effective than limestone in raising the protein concentration of the herbage in the enclosed hill *Festuca-Agrostis* area. On the open hill *Festuca-Agrostis* area limestone gave a slightly higher yield of protein than superphosphate. At the *Molinia* centre the superiority of limestone over superphosphate in its influence on protein productivity was outstanding. At this centre the limestone treatment alone was as effective as the joint influence of potash, phosphate and nitrogen.

The different treatments were even more effective in raising the lime and phosphate yield than in increasing protein productivity. If the yield of protein from a single cut on the control plot be taken at 100 lb., the maximum yield from a single cut following treatment amounted to 1955 lb., while the maximum yields of lime and phosphate for every 100 lb. of these ingredients produced on the control plots amounted to 4625 and 6550 lb. respectively. The effect of limestone on the yield of herbage lime at the two *Festuca-Agrostis* areas has been similar to that of superphosphate, but the herbage lime yield at the *Molinia* centre has been influenced to a much greater degree by the limestone than by the superphosphate. Limestone has been more effective in increasing the pasture lime yield at all centres than complete fertilizer treatment without limestone.

At the *Festuca-Agrostis* centres superphosphate had a greater influence on herbage phosphate productivity than limestone, but at the *Molinia* centre the influence of the limestone was slightly greater than that of superphosphate.

Some of the effects of the treatments on the soils at the three centres are discussed. In contrast to the small influence of the fertilizers, limestone has been effective in diminishing the acidity at all centres. The soil of the control plots had a *p*H range of 3·99–4·80 compared with a *p*H range of 5·23–6·12 in the limestone-treated plots, and this diminished acidity was accompanied by a marked increase in exchangeable lime.

The grazing animal was found to be an important factor in contributing towards a high ratio between the lime recovered in the herbage and that leached from the soil. In hay plots treated with limestone and complete fertilizer the total mean annual loss of lime (CaO) from the soil amounted to 217 lb., only 9 lb. of this being recovered in the herbage. In the plots similarly fertilized but subjected to controlled grazing, the mean total annual loss of lime from the soil amounted to 211 lb., 59 lb. of this being returned in the herbage.

The application of potash salts and of superphosphate raised the available potash and the available phosphate in the soils at the three centres. The potash applied to the soil was rapidly absorbed by the herbage, and the effect of the grazing animal was evident in that the amount of potash found in the herbage exceeded that applied in the fertilizer. The phosphate recovered in the herbage amounted on the average to 71·6% of that applied in the fertilizer, a large proportion of this being due to the heavy manuring of the plots by the sheep.

The outstanding feature of these results from a chemical standpoint is the cumulative effect that fertilization and grazing have produced on the nutrients derived from natural hill pastures. The volunteer species that have gradually taken a dominant place in the vegetation as a result of continuous and generous treatment have effected a marked increase in concentration and yield of protein, and this has been accompanied by a great drift in concentration and yield of minerals towards higher levels. These nutrients have been increased to a degree that would be impossible from the fertilization alone, and they are largely the outcome of the intensive manuring of the grazed plots by the sheep. The net result of the defoliation and manuring by sheep on the fertilized plots is not only a volunteer herbage radically different from the old natural sward in nutritive value, but also a soil richer in those available constituents necessary for the future maintenance of the better quality herbage.

These changes in the herbage and the soil can be successfully accomplished with judicious management under exceptionally adverse conditions. Several constituents in the various fertilization treatments have contributed towards concentration and yield of nutrients, but of all the elements provided calcium has proved the most important single factor. It is evident that the provision of calcium has brought the volunteer species within profitable reach of certain forms of animal and soil phosphorus and of atmospheric, animal and soil nitrogen which in the absence of adequate calcium supply would be inaccessible to the plants. It is also clear that the success of the volunteer species has led to the conservation of a considerable proportion of the calcium supply that played such a vital part in their establishment.

ACKNOWLEDGEMENTS

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A NOTE ON A CONNEMARA BOG TYPE

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(*With two Figures in the Text*)

The data presented here primarily represent an attempt to extend further some previously recorded observations on peat *p*H values in relation to vegetation distribution (Pearsall, 1938). In interpreting such observations it is convenient to distinguish extreme types, and the particular purpose of the observations now recorded was an objective description of the vegetation and the determination of the soil characters developed under extremely wet climatic conditions. It is obvious that in dealing with factors affecting soil humidity, slope must always be of prime importance and, consequently, in seeking to describe the extreme Connemara bog type, we confined our observations chiefly to areas (1) with gentle slopes, less than 1 in 20, (2) with high rainfall.

One of the most characteristic areas is that between the Twelve Bens and Maam Turks. The bogs at Nacarrigeen and Kylemore are representative of this area, spreading as they do over gently undulating ground. The Kylemore bog also occupies the bottom of the valley at the inlet end of the upper lake, and on this site it presents the appearance of a "raised" bog. This part of the bog was particularly examined as representing an extreme western example of this type of site. A comparison was made of the vegetation of the valley bottom and that of the adjacent slopes. Topographically, the Doo Lough bog resembles that at Nacarrigeen. It covers undulating ground at the north-western end of the Doo Lough (see Fig. 1). All these localities must be closely alike in their climatic conditions and must experience a rainfall of the order of 240-252 cm. (95–99 in.), the averages at Aasleagh House and Delphi Lodge with similar altitudes and exposures. Praeger (1934) gives an older 16-year average of 208 cm. (82 in.) for Kylemore Castle at the western and more open end of the Kylemore valley, but the rainfall above the loughs is almost certainly greater than that at the castle.

The other station at Shinanagh lies outside the zone of extremely high rainfall in the mountains. It is a bog lying at an altitude of about 115 m. on the low and broad shoulder of a hill between Letterfrack and Clifden. There is a small holding with pastures above it on the steeper slopes (*ca.* 1 in 10), and the bog undoubtedly owes its existence to topography and possibly to a small lake in the first instance. It is a very good example of a growing bog in the far west. The rainfall at Ballynahinch, which is a place of similar exposure but lower altitude (13 m.), is about 152 cm. (61 in.), and on this basis Shinanagh can hardly average less than 175 cm. or nearly 70 in.

The records given for these places were obtained in early August 1939. The species lists are those for five or more representative quadrats (each 1 sq. m.) from each area. The *Sphagna* were verified by Mr A. Thompson to whom we are much indebted. Soil samples from the representative quadrats, carefully packed to fill the sample tins and maintain the original packing and aeration, were transported to England, some with and some without toluol. The *p*H was determined electrometrically in suspensions of soil in water (approximately 1 in 3 by volume) saturated with quinhydrone (see Pearsall, 1938). The *p*H of both outside and inside of the peat samples was determined to see if much oxidation had ensued in transit. There was no significant difference. The *p*H values obtained are given in Tables 2 and 3. Table 1 summarizes the vegetation of the areas examined. In this table, each column gives the number of metre quadrats in which the given species was observed. *Calluna* was present in all of the quadrats. Column 6 is ignored in obtaining the percentage occurrences given in the last column.

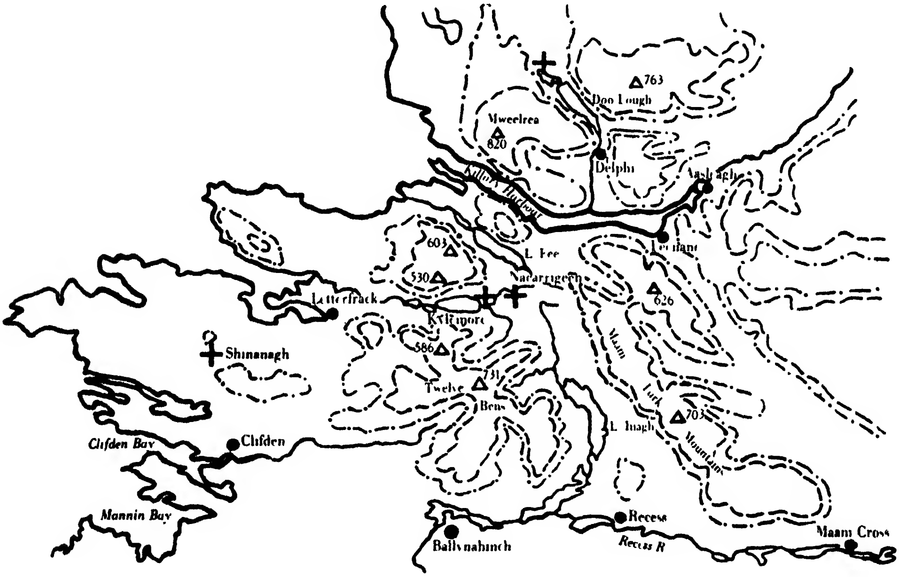

Fig. 1. Map showing localities mentioned in the text, the crosses indicating the bog sites described. Heights are given in metres, the contours being 150 and 300 m.

It has already been stated that the main comparison made was between the vegetation of the gentle slopes as at Nacarrigeen and of the valley bottom at

Kylemore. These bog systems are continuous, though Nacarrigeen is about 1 km. farther east than the best transect of the Kylemore bog. Ten quadrats are recorded for the former area and fifteen for the latter. The Kylemore quadrats were taken on a transect from the hillside (end of the slope) across the valley at 50 m. intervals. The first five (phase I) occurred on what was a rather more spongy continuation of the hillside bog farther east. After moving 300 m., however, the quadrats tended to fall into wetter and drier types as a definite microtopography developed. Consequently they were taken in pairs, representing the higher and lower levels of phase II of this bog. The general arrangement of this microtopography and its vegetation is shown in Fig. 2.

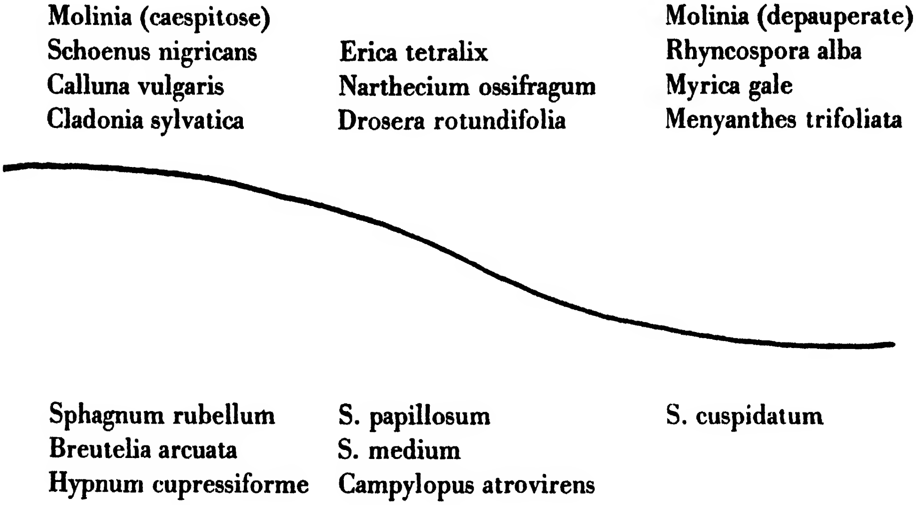

Fig. 2. Arrangement of species in relation to microtopography.

The resemblance to that of a "raised" bog (cf. Tansley, 1939, p. 688) is evident, although the species are different. It appears probable that the existence of this feature was associated with some drainage effects, as the eroded edge of the peat was roughly parallel to the transect at about 100 m. distance, the transect lying down the middle of a broad tongue of peat.

The comparison of the vegetation of these three phases is given in Table 1, and from this table it is possible also to note the close general resemblance between the wetter parts of the Kylemore bog and the actively growing bog at Shinanagh. It seems justifiable to suppose that all these examples belong to one vegetation complex and, accordingly, we may treat them as such.

It is clear from the lists given in Table 1 that many species are constantly present in the sample areas taken. Each square metre will normally contain *Molinia caerulea*, *Erica tetralix*, *Calluna vulgaris*, and *Sphagnum* spp., while 70% of the quadrats or more will also contain *Schoenus nigricans*, *Rhyncospora*

Table 1. *Species present in representative areas*

	1. Nacarrigeen	2. Kylemore, phase I	3. Kylemore, phase II drier	4. Kylemore, phase II wetter	5. Shinanagh	6. Doo Lough, burnt	Percentage 1–5
Calluna vulgaris	10	5	5	5	6	5	100
C. panicea	2	1	.	.	.	2	14
Drosera anglica	2	2	.	2	3	3	26
D. intermedia	1	1	.	1	.	1	10
D. rotundifolia	8	5	4	4	4	3	81
Erica tetralix	9	5	5	5	5	5	94
Eriophorum angustifolium	7	5	1	1	.	3	45
E. vaginatum	.	.	.	.	1	.	+
Juncus bulbosus	1	.	.	.	.	.	+
J. squarrosus	.	.	.	.	.	1	.
Menyanthes trifoliata	1	3	1	5	6	.	52
Molinia caerulea	10	5	5	5	5	5	97
Myrica gale	3	2	1	5	4	.	48
Narthecium ossifragum	8	3	1	4	6	4	71
Pedicularis sylvatica	1	1	1	.	.	.	10
Phragmites communis	1	.	.	.	3	.	13
Pinguicula lusitanica	.	1	.	.	.	.	+
Polygala serpyllacea	1	.	1	.	.	.	6
Potamogeton polygonifolius	.	.	.	.	3	.	9
Potentilla erecta	2	1	1	.	1	.	13
Rhyncospora alba	9	5	1	5	5	4	81
Schoenus nigricans	8	5	5	2	5	5	81
Scirpus caespitosus	2	.	1	.	.	.	10
Utricularia minor	.	.	.	2	.	.	6
U. intermedia	.	.	.	.	1	.	+
Breutelia arcuata	1	1	3	2	1	.	26
Campylopus atrovirens	3	4	.	3	3	5	42
Hypnum cupressiforme	.	1	1	1	1	.	13
Leucobryum glaucum	1	.	.	.	.	.	+
Pleurozia purpurea	3	5	3	5	3	.	61
Rhacomitrium lanuginosum	5	4	3	1	2	1	48
Sphagnum auriculatum	.	1	.	.	1	.	+
S. centrale	1	2	.	1	2	.	19
S. cuspidatum	4	2	.	3	4	.	42
S. cymbifolium	2	1	1	1	.	.	16
S. imbricatum	.	1	.	1	1	.	+
S. medium	1	2	1	1	1	.	20
S. obesum	.	1	.	.	.	.	+
S. papillosum	7	5	2	5	5	1	77
S. plumulosum	3	1	2	1	2	.	32
S. rubellum	6	4	5	3	4	.	70
S. tenellum	1	1	1	1	.	.	13
Cladonia sylvatica	4	3	4	.	1	1	39
Cladonia *spp.*	2	.	1	.	.	.	10
Zygnema ericetorum	.	2	.	1	.	.	10

alba, *Narthecium ossifragum*, *Drosera rotundifolia*, *Sphagnum papillosum* and *S. rubellum*. Other species occurring in more than two quadrats in five are *Eriophorum angustifolium* (curiously scarce on phase II and at Shinanagh), *Myrica gale*, *Menyanthes trifoliata*, *Sphagnum cuspidatum*, *Campylopus atrovirens*, *Pleurozia purpurea*, *Rhacomitrium lanuginosum* and *Cladonia sylvatica*. There is thus a very large number of species per unit area, the average is 13·7 per sq. m.

These figures give a fairly good idea of the relative abundance of the most noteworthy species as well as what they show most exactly, the constancy of occurrence of these species. Few of the plants grow luxuriantly, and this is perhaps most marked in the cases of *Molinia*, *Calluna* and *Schoenus*, all normally represented by depauperate forms. The robust and caespitose forms of *Molinia* and *Schoenus* appear to be found only where drainage and oxidation occur. Where a definite microtopography is developed, *Schoenus* shows a decided preference for the tops of the hummocks.

The wetter places on these bogs are characterized by *Myrica gale*, *Menyanthes trifoliata*, *Utricularia minor*, *Sphagnum cuspidatum* and *S. cymbifolium*. Otherwise the greatest variations in the vegetation appear to be due to changes in the degree of *Sphagnum* cover, and the phanerogam vegetation is fairly constant in composition whether the locality is sloping or is apparently developed from lacustrine peats. The main difference in the latter case is that the surface is more spongy and the *Sphagna* more luxuriant. The *Sphagnum* cover is, however, more or less continuous over most of the area and rarely covers less than one-tenth of each quadrat, a high proportion when the number of other species and their varied habit is considered.

In the hollows and on the wetter bogs the *Sphagnum* cover is only interrupted by the emergent shoots of higher plants. The Doo Lough bog, however, is markedly different because *Sphagna* are practically absent and the peat surface is visible. This is because this area has been burnt and probably all of it within the last three or four years, and possibly more than once. The disappearance of the *Sphagnum* cover is obviously associated with the desiccation and oxidation following burning. The exposure of the peat surface resulting from the absence of bryophytes further tends to increase the effects in the years following the operation. Similar effects are shown on parts of the Nacarrigeen bog which have been burnt, although there the effects on the *Sphagnum* cover are far less extreme.

Another noticeable feature of the Doo Lough bog quadrats is the absence of such species as *Menyanthes trifoliata*, *Myrica gale*, *Phragmites communis* and *Pleurozia purpurea*. This may also be due to the changes following on burning. The presence of these plants in many of the Connemara bogs is important, not because it necessarily implies that the bogs have originated from lakelets, but because it shows that the normal absence of soil desiccation is a permanent feature of the habitat.

SOIL CONDITIONS

The soil acidities recorded for the peat samples are given in Table 2. In general the *p*H values recorded are high and are usually above 4·7. This figure was about the average for the typical Nacarrigeen bog, and was also that obtained for the driest places on the Kylemore bog—the hummock tops. Most of the samples from Kylemore, particularly in the depressions, gave higher values, above 5, as also did the wet Shinanagh bog. It may, therefore, be assumed that the *p*H of the bog peats is normally above 4·7. It will, however, be seen from the table that the Doo Lough bog gave lower *p*H values. Still lower values were obtained from the burnt areas on the Nacarrigeen bog. It is, therefore, suggested that the drying following on burning leads to oxidation and to increase in peat acidity. Another noticeable feature of the soil samples was the smell of sulphuretted hydrogen from the wetter Kylemore and the Shinanagh soils, indicating the presence of processes of reduction. These only predominate in waterlogged and oxygen-deficient soils.

Table 2. *The* p*H values of typical bog soils*

Locality	*p*H values
1. Nacarrigeen, typical	4·78, 4·75
2. Kylemore, phase I	5·46, 5·06
3. Kylemore, phase II wetter	5·38, 5·35
4. Kylemore, phase II drier	4·72, 4·66
5. Shinanagh	5·31, 5·12
6. Doo Lough, burnt	4·84, 4·44
7. Nacarrigeen, burnt	4·23, 4·18

Samples from 2, 3 and 5 smelled of hydrogen sulphide.

The high *p*H of these peats is attributed to their waterlogged character and to lack of oxidation. There seems to be no need to believe that the soils have some external source of bases (sea spray has been suggested) which prevents the development of a low *p*H, for the soils are base-deficient in any usual sense of the term. Consequently, when they are allowed to dry out slowly in the laboratory, oxidation takes place and there is nothing to prevent the development of high hydrogen ion concentrations, akin to and even greater than those observed in acid peats which are not permanently waterlogged. This is illustrated by the figures in Table 3, which represent the *p*H values obtained when some of the Connemara peats were allowed to dry slightly at room temperature in the laboratory for 14 days.

Table 3. p*H values of bog peats before and after partial drying in air at room temperature for* 14 *days*

	Before	After
1. Kylemore peat, normal sample	5·46	3·25
2. Kylemore peat, hummock top	4·72	3·27
3. Nacarrigeen, normal peat	4·75	2·53
4. Nacarrigeen, burnt area	4·18	3·44
5. Doo Lough bog, burnt	4·44	3·07

All of the samples gave, after oxidation, *p*H values of the same order as the most acid peats commonly found in the British Isles, while one sample, No. 3, gave a *p*H of 2·53, well below any value recorded for peats in nature. It is noticeable that the peats from burnt areas gave proportionately small increases in hydrogen-ion concentration.

CONCLUSION

The data given show that the bog type developed under these extremely wet climatic conditions is fairly uniform both in vegetation and in edaphic characters. The high peat *p*H is that characteristic of a waterlogged and base-deficient soil, and does not indicate the presence of bases. The peat is deep and, under the high rainfall conditions, sites which in drier climates would develop "raised" bogs show a vegetation not materially different from that of the neighbouring slopes. Undoubtedly this general type of bog has a wider distribution than is indicated here. Similar examples have been recorded from the gentle slopes south of Maam Cross, and good examples of closely similar composition were seen in Donegal on similar terrain. We have limited the examples to those for which reasonable estimates of rainfall could be given. Hence we may say that the type of bog described develops in districts where the average annual rainfall is probably between 230 and 255 cm. on extensive slopes of less than 1 in 20. It appears to be always on deep, base-deficient and waterlogged peat with a *p*H above 4·7.

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STUDIES IN SALT-MARSH ECOLOGY
SECTION VIII

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(*With seven Figures in the Text*)

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INTRODUCTION

IN the opinion of the present author a complete understanding of the successional stages in salt-marsh vegetation cannot be achieved until the autecology of the dominant species has been thoroughly worked out. Autecological studies of certain salt marsh species are being undertaken at present but it is not anticipated that these will be concluded in the near future. It is, therefore, proposed to terminate the present series by an account of the salt-marsh succession in Norfolk together with a brief description of the marshes generally around our shores. Recently Tansley (1939) has suggested that the salt-marsh vegetation should be regarded as a formation, that is, a piece of vegetation that represents a climax in the conditions under which it exists. The present author does not feel that he can subscribe to this view although professing a great respect for Tansley's knowledge and experience. Salt-marsh vegetation is essentially dynamic, and whether the succession is apparently terminated by a Juncetum maritimae or Juncetum Gerardii depends on a number of factors. In those areas where fresh water flows out to sea there would seem little doubt that salt marsh progresses to reed swamp, and further development by way of carr to the woodland climax is theoretically possible. I have believed for some time that the fens have developed in this manner, and this view has also been expressed by Godwin (1940). A similar transition to reed swamp has also been recorded from the North American marshes by myself and other authors (1940). A Juncetum maritimae, therefore, can at the best only be regarded as a sub-climax and not a climax. A further consideration must be associated with the relative movements of land and sea. If the land is rising in relation to sea-level, then sooner or later the halophytic vegetation will give way to normal land vegetation, the further development of which will depend on whether it is left untouched by man or not. It is not improbable that such conditions are to-day obtaining on the marshes north of the line Humber-Mersey. On the other hand, if the land is sinking, marsh development will take one of two courses.

A. If silt deposition is equal to or greater than the rate of change of level, the marsh succession will still be found although progression to normal land vegetation will be unlikely. However, it hardly seems justifiable to regard such a state as representative of a climax and as a result to invoke the formation concept. It is probable that such conditions may to-day be existing south of the line Humber-Mersey.

B. If silt deposition is less than the rate of change of level, the marshes will commence to undergo a retrogressive succession and will finally disappear.

The most satisfactory interpretation of the salt marshes would seem to be that which regards them as a number of different seres, all of which are potentially capable under proper conditions of developing to the climatic or edaphic climax, which in the case of Great Britain would be deciduous woodland or coniferous forest in sandy areas. In many places, however, these seres are inhibited by local factors from proceeding towards the climax. The present author is of the opinion that the salt marshes of Northern Europe all represent a number of different seres potentially proceeding towards a normal climax, and later in this section four such seres will be described from Great Britain.

NORFOLK SUCCESSION

The different communities that are to be found on these marshes have already been described elsewhere (1934), and it remains to indicate their relationships to each other and the general succession.

Observations along the Norfolk coast show that the marshes appear to develop in two directions. When the mainland is protected physiographically from direct wave action, marshland will grow out slowly from the shore and spread seaward, the rate of extension being determined to some extent by the degree of protection, although the amount of silt available must also be important. Off-shore bars are quite a common feature along this coast (Steers, 1936), and it is behind such structures that another type of salt marsh develops and gradually extends landwards until it meets the marsh advancing from the mainland. Apart from this fundamental difference in origin there is also a difference in the type of soil. The soil of the marsh advancing from the mainland contains a high proportion of silt, whereas that of the marsh advancing landwards from the off-shore bar has a high proportion of sand. The off-shore marsh is formed primarily upon the sand beach, as may be seen behind the West island at Thornham, but sand is also continually being deposited from the beach in front and from the sand dunes which sooner or later develop upon the off-shore bars. At present the best example of these two types of marsh is to be seen at Thornham, but I believe that the marshes behind Scolt Head Island have undergone essentially the same development. The bare patch on the Hut marsh, for example, probably represents the final stage in the colonization of the bare ground between the two types of invading marsh. In general the marsh advancing from the mainland will do so at a greater rate than that developing behind the protection of the dunes, and it will therefore extend over a greater area. The reasons for this are:

(1) The mainland marsh series will commence development long before the one behind the off-shore bar because it may be some time before conditions are favourable to bar formation.

(2) The embryo bars are by no means stable and are liable to be moved or washed away, and hence marsh development may be stopped or transferred to another area.

(3) The sandy substrate does not provide such a good soil for seedling establishment because of its liability to wind and water erosion. On the flat sandy shores of Norfolk a series of off-shore bars has developed in the past and formed behind them.

It is probable that such conditions were realized in the mainland marshes behind Scolt Head Island where the Nod forms a small off-shore bar and there are others, still older, nearer the sea wall. The youngest stages were to be seen a few years ago between Wells and Morston where mainland marsh was progressing seawards and small bars were forming on the beach in front, but these were not big enough then to afford sufficient protection for off-shore marsh formation to commence. One further interesting feature of these marshes is the behaviour of *Glyceria* (*Puccinellia*) *maritima* which, as a primary colonist, is extremely rare and only occurs where the soil is very sandy. A *Glyceria* marsh has, however, developed at the eastern end of the golf course at Brancaster, and marshes bearing sea meadow (Glycero-Obionetum) always have a very muddy soil. There are other places, e.g. in front of the advancing Wells and Thornham marshes, where one would expect to find *Glyceria* as a primary colonist, and yet it is absent even though the conditions appear to be such that, if the marsh were on the West coast of England, *Glyceria* would certainly be the primary colonist. This provides a problem to which at present no satisfactory answer can be given, nor is one likely to be available until the autecology of the species concerned has been investigated. On the other hand, *Glyceria* forms a very effective colonist of old creeks where the soil is very damp and drainage presumably good. On the mature mainland marshes behind the

Nod the outlines of former creeks are clearly marked by the areas of *Glyceria*. Similarly the plant is also an excellent colonist of pans, although in this process other species such as *Salicornia herbacea* (agg.) and *Suaeda maritima* may take part.

It is generally supposed that the primary succession on a salt marsh is a relatively simple affair, and it has been thus presented in Tansley's recent book (1939). The present author, however, is of the opinion that salt-marsh succession is anything but simple, that it is not only complex in any one given region, but that there is considerable local variation in the different seres that are to be distinguished.

The scheme of Fig. 1 calls for but little comment. For convenience the succession found on pans that are being colonized is segregated into two sections. The primary succession with the various alternatives forms the main left-hand column, and this represents the type of succession that one finds in the marshes that are developing seawards from the mainland. The other principal succession which is found primarily behind the off-shore bars that bear sand dunes is shown in the main right-hand column, and it is probably determined to a large extent by the percentage of sand in the soil. The exact status of Spartinetum strictae is difficult to assess. Prof. F. W. Oliver informs me that in 1920–1 there were three plants on Missel marsh at Scolt, and now there are three considerable patches which are obviously spreading. There is also a very large patch on the Great Aster marsh and another on the mainland opposite Plover marsh. It would seem from observations on the latter that it will give way to some form of general salt marsh.

THE SALT MARSHES OF THE BRITISH ISLES

The accompanying map (Fig. 2) marks the areas of salt marsh which have been visited and studied by the present author or which have been described very fully by previous workers. It is not pretended that these represent all the marsh areas of Great Britain but sufficient have been visited to yield a general picture. The marshes fall into four groups each developing along different lines and under different conditions, but in spite of such differences they ought properly to be regarded as parallel seres all potentially capable of progressing to the climatic or edaphic climax.

EAST COAST MARSHES

A scheme (Fig. 3) has been prepared from observations made on these marshes and, although it is very complex, I believe it is a fair representation of the type of succession that may be encountered on the marshes. It is not suggested that all the variations are to be found on any one marsh area, and it cannot be too strongly stressed that any line of development may be shortened or lengthened through the influence of local conditions. In Essex old reclaimed marshes that were invaded anew by the sea around 1932–3 are now covered primarily by *Glyceria maritima* with *Salicornia* spp. and *Aster tripolium* in the lower areas. In small areas such as Holme in Norfolk, where one small marsh

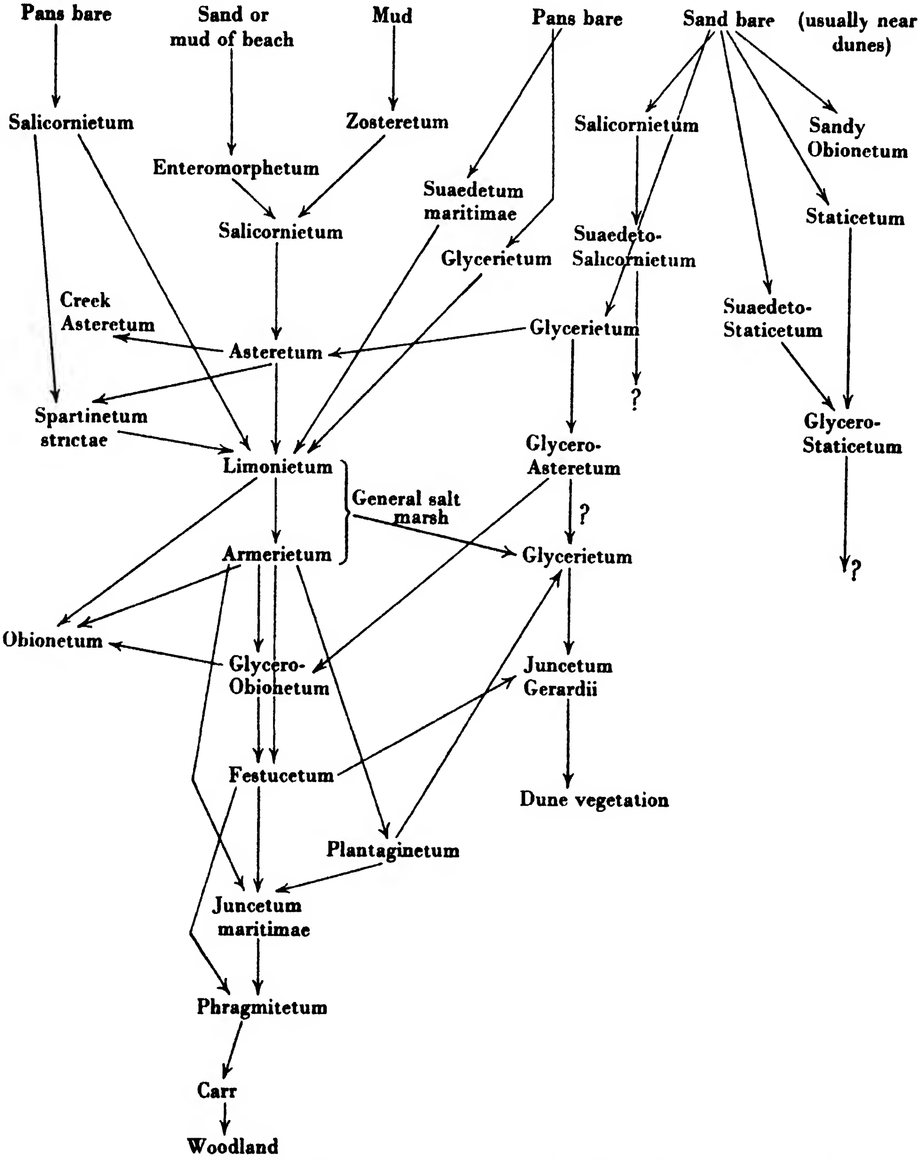


Fig. 1. Salt-marsh succession in Norfolk. (For a description of the communities see Chapman, 1934, 1938.)

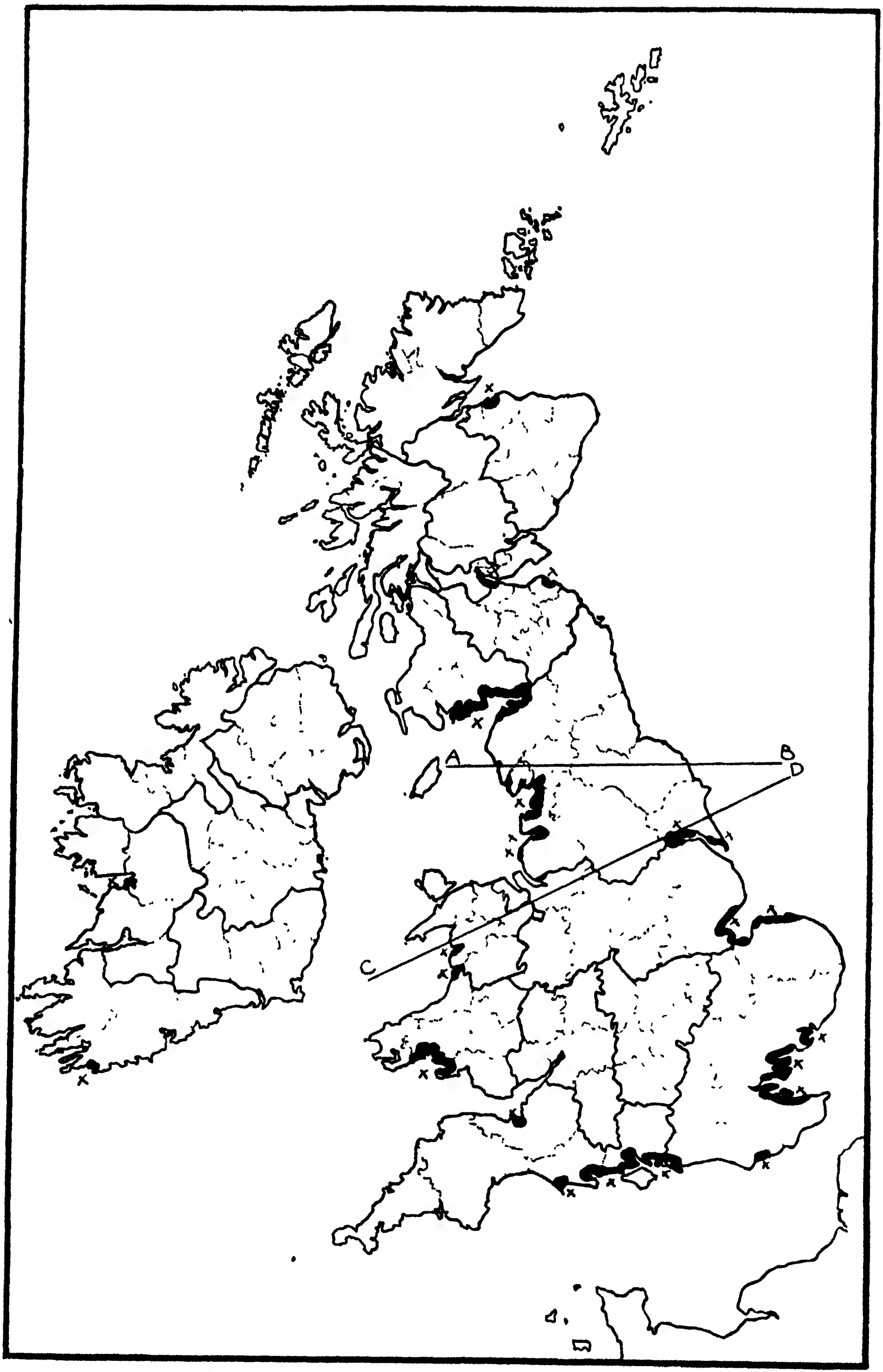


Fig. 2. Major salt-marsh areas of Great Britain. AB. Northern limit of abundant *Obione portulacoides* and *Aster tripolium* var. *discoideus*. CD. Northern limit of natural (?) *Spartina Townsendii*.

has developed very rapidly on account of its closed character, the succession is very much compressed and somewhat difficult to disentangle. Around the

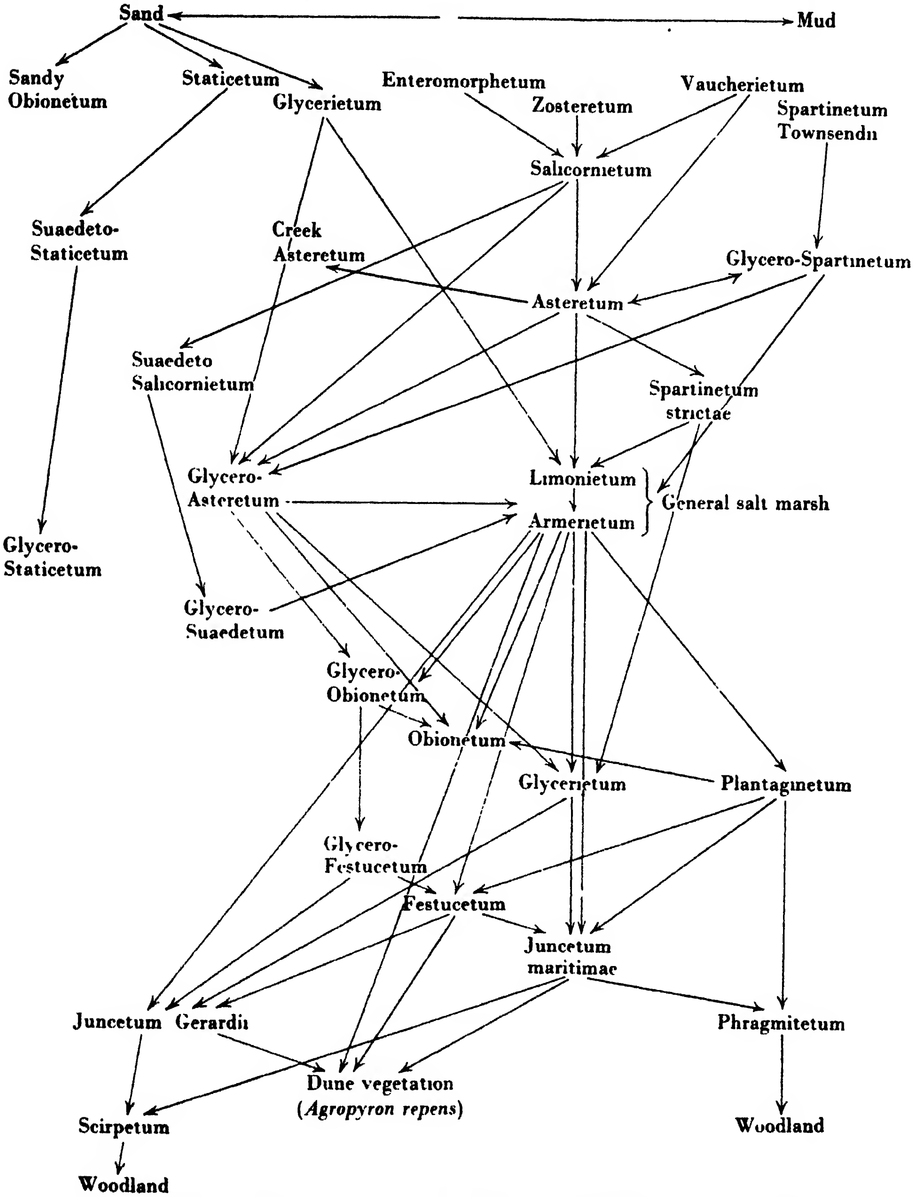


Fig. 3. East coast sere. The actual course of the sere depends on local conditions.

bottom of the Wash, e.g. Nene outfall, the land is more sandy and *Glyceria* is the primary colonist, although close by, at Ongar on the west bank of the Ouse, *Spartina Townsendii* appeared in 1925 (according to local information) and now covers large areas. The farmers are grateful for the protection it has afforded to their sea walls, but if it spreads seawards rapidly, as it appears to be doing, it may interfere with navigation on these already shallow waters. In South Lincoln the true marsh is only a narrow belt, and in 1919 Newman and Walworth suggested that the land vegetation was invading the upper marsh areas. The Humber marshes are interesting because they mark the northern limit on the east coast of *Obione portulacoides* in any abundance and also of the rayless form of *Aster tripolium* (var. *discoideus*). The marshes at Aberlady and Dunbar are of unusual interest because of the frequent occurrence of marsh fucoids which are apparently entirely absent between here and the Wash. The zonation at Dunbar is probably determined by the greater proportion of sand in the soil. Summing up one may say that the principal features of this east coast sere are:

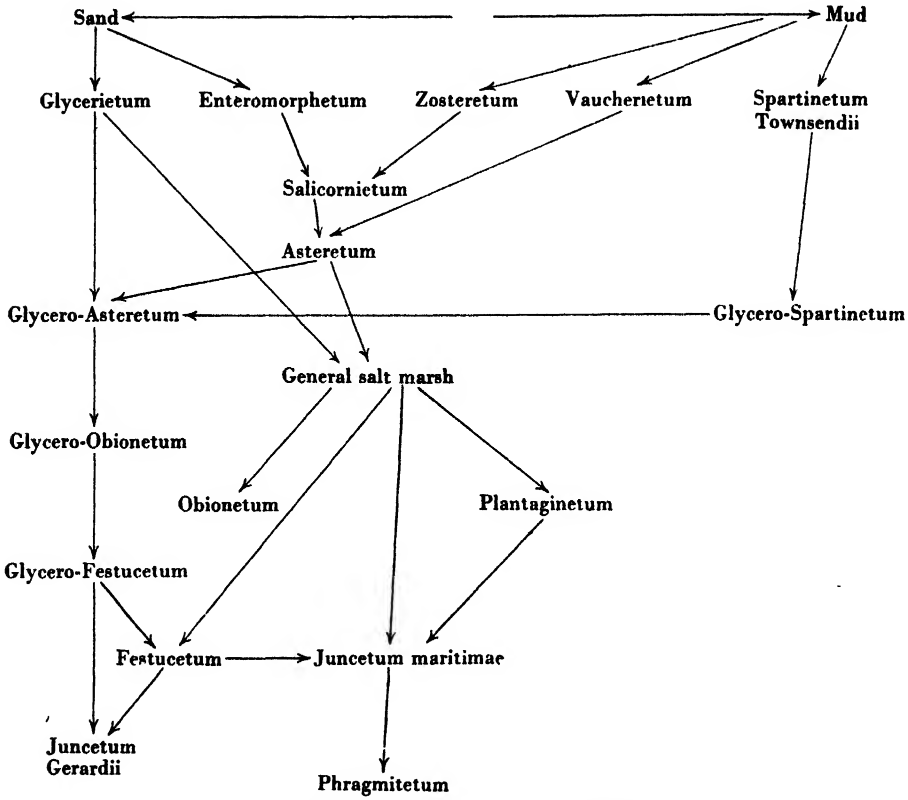


Fig. 4. Simplified schema of an east coast sere.

(1) Local development of *Spartina Townsendii* and *S. stricta*. The former only does really well at Ongar in the Wash and on the Kent marshes, whereas the latter is at its best on the Essex marshes.

(2) Dominance of *Glyceria maritima* occurs only in the regions where there is much sand admixed in the soil.

(3) A great number of consocies can be recognized and the flora as a whole is very varied. The actual extent of the General salt-marsh consocies on the marshes and its central position in the sere is a characteristic feature.

(4) The soil is generally very muddy but is often quite firm in contrast to that of the south coast marshes.

(5) Because of the thick clay soil much of the marsh land is excellent material for enclosure when it forms good pasture. On the whole the wild marsh is poor grazing because the grasses do not cover the large areas that they do on the west coast marshes.

(6) There is usually a rich algal flora, and, in particular, the abundance of the salt-marsh fucoids is a very characteristic feature. The Norfolk marshes together with the Irish marshes might be regarded as the home of the marsh fucoids.

(7) *Obione portulacoides* is a very typical plant of these marshes, especially along creek banks.

South coast marshes

These extend over a much smaller area of coast-line and, although the present author so far has not had an opportunity of visiting the marshes along the north coast of France, nevertheless it might be expected that they would belong to this sere. The primary colonist now is usually *Spartina Townsendii*, but before the appearance of this hybrid at the end of the last century the other two species of *Spartina* probably fulfilled this role. In one region (Cuxhaven) *Salicornia herbacea* agg. is the pioneer species, and its absence in other areas may be due to a lack of a relatively stable substrate in which it can become established. Occasionally an Enteromorphetum may precede the Spartinetum. Behind the Keyhaven marshes lie some salterns or old reclaimed marshes that became flooded once more through the breaching of the sea wall in 1937. In 1938 plants of *Juncus maritimus* and *J. Gerardii* covering the salterns were dying, presumably because of lack of adequate aeration due to the permanent standing water. On more elevated areas annuals such as *Salicornia herbacea* agg., *Suaeda maritima* and *Atriplex patula* var. *hastata* were common. There were other reclaimed marshes at Calshot, and here it was interesting to note that the beds of the old creeks had been colonized by *Spartina Townsendii* and that a peaty soil was developing, whilst along the edges there was a relict flora of *Juncus maritimus* and *J. Gerardii.* Another example of peaty soil was to be found in Poole Harbour under stands of *J. Gerardii*, but in neither case was the peat as compact as that recorded from Ireland. In Lytchett Bay there are large areas of *Scirpus maritimus* and

Phragmites communis, and amongst them there are to be found more elevated areas bearing remains of a Juncetum (*J. maritimus* and *J. Gerardii*). This region was also interesting because the Phragmitetum gave way to a freshwater bog very comparable to some successions described from the New England marshes (Chapman, 1940).

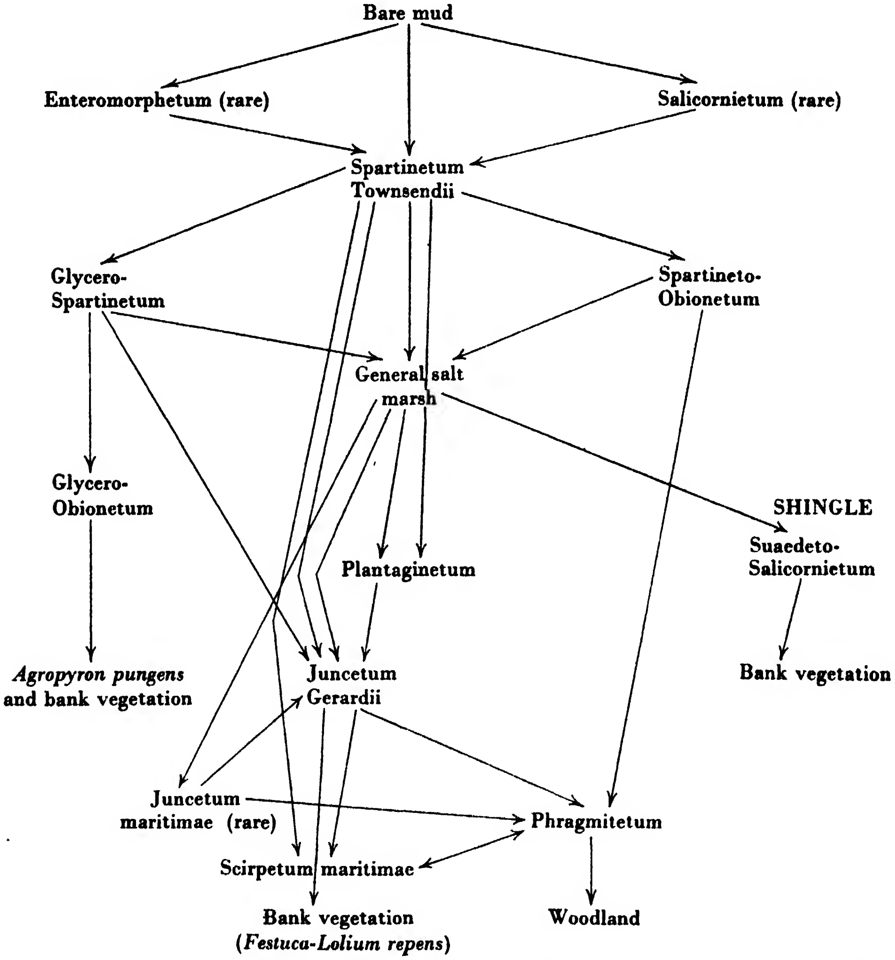


Fig 5. South coast sere. Any line of development may be shortened through local conditions.

The principal features of this sere are:

(1) The enormous areas covered by *Spartina Townsendii.*

(2) The soil is a very soft mud except near the borders of a marsh.

(3) *Obione portulacoides* is not common and when present is usually confined to the creeks.

(4) Algae are sparse on the marshes, probably because the dense *Spartina* does not permit of adequate light conditions. Although there are abundant

fucoids present in the vicinities of these marshes, nevertheless in only one area, the Chichester Channel, has the present author found any marsh fucoids. In the schema (Fig. 5) it is probable that the Spartineto-Obionetum and Glycero-Spartinetum represent ecotones, but further work is required before this can be established.

WEST COAST MARSHES

The sere on this portion of our coast-line is relatively simple when compared with the two already described. The general appearance of the marshes is determined by the dominance of *Glyceria maritima*, whilst another characteristic feature is the undercutting of the creek banks which then subside and become invaded by species from lower levels so that secondary marsh development can be observed. As a result of this undercutting the large creeks become partially colonized, the courses narrowed and in many cases even covered by a bridge of *Glyceria* turf. In South Wales, on the Penclawd and Kidwelly marshes, it seems that grazing determines the extent of *Obione portulacoides*, because on the grazed areas it is more or less confined to the creek banks, whilst on the ungrazed portions it is present over the whole marsh. It is possible that the slow growth of *Obione* seedlings does not enable the species to tolerate continual cropping and the plants, therefore, cannot become established except along creek banks which are avoided by the sheep. On the marshes of West Wales, *Glaux maritima* is often dominant in areas where water tends to accumulate, and such places appear to be comparable to the lows of Norfolk dunes. *Spartina Townsendii* is recorded from near Dovey, the plants having arrived naturally from a planted area up an estuary in the neighbourhood. However heavy the grazing on the main marsh, the Juncetum is always left untouched, and it is commonly only in this zone that the marsh plants can reach the flowering stage. The marshes at Morecambe represent the northern limit on the west coast of *Aster tripolium* var. *discoideus* and also of *Obione portulacoides* in any abundance. The marshes along Solway Firth appear to be rising in relation to sea-level because now the bulk of the land is only flooded by storm tides, and this observation conforms with the view that north of the Humber and Mersey the land is rising in relation to sea-level whereas south of that line it is sinking. A characteristic feature of these marshes are the terraces which can be observed, sometimes as many as three on an individual marsh. It is probable that they are related to past movements of the main channel. A study of the marshes at Findhorn in Nairnshire and Morayshire suggest that they fall into the west coast sere rather than into that of the east coast, primarily because they are forming upon a very sandy soil. It should be clear from the descriptions of these seres that the type of soil plays a very large part in determining the general type of vegetation to be found on the different marshes. These conclusions are represented very diagrammatically in Fig. 7, and it is hoped that further work upon the composition of the soils will yield even more conclusive evidence. The principal features of these marshes are:

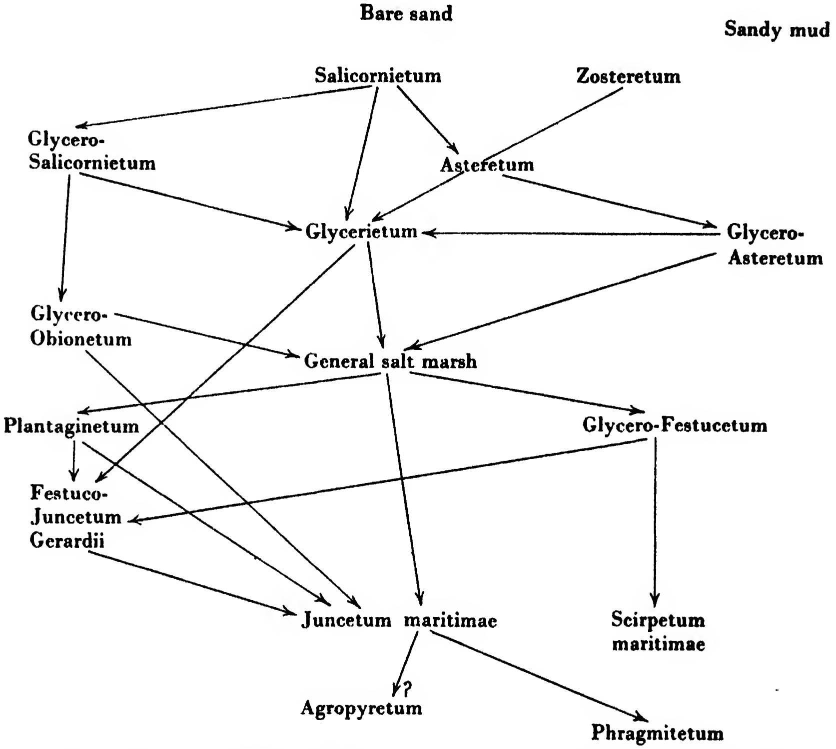


Fig. 6. Schema of west coast sere. Any line of development may be shortened through local conditions.

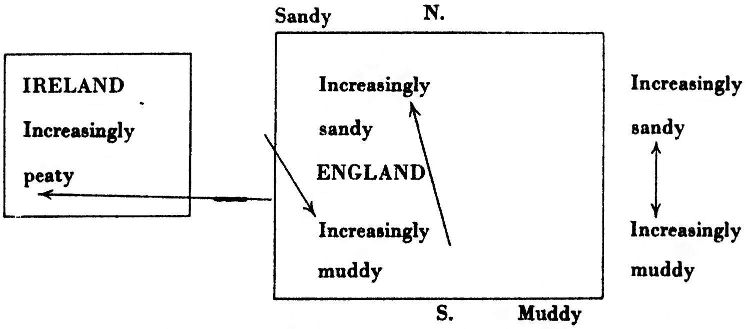


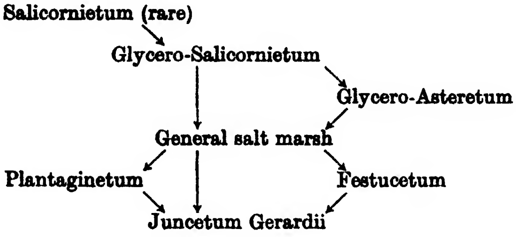
Fig. 7. Soil tendencies in the salt marshes of the British Isles.

(1) The very sandy soil with *Glyceria maritima* nearly always the primary colonist.

(2) The succession is dominated throughout by *Glyceria*, and hence these

marshes are particularly suitable for grazing. On account of the very sandy soil, however, they do not form such good material for enclosure as the more muddy marshes of the south and east coasts.

It is perhaps of interest to point out here that the salt marshes at Skallingen on the west coast of Denmark bear a very close resemblance to the west coast marshes of England. It might have been anticipated that they would resemble most the marshes on our east coast, but the very sandy nature of the soil is the principal reason why they do not. That there is a similarity to the west coast sere can be seen from the successional stages that have been observed on these marshes by myself and Iversen (1936).



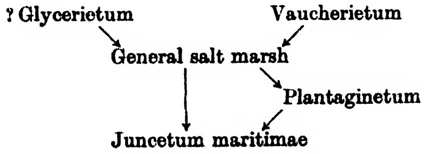
IRISH MARSHES

Very little is known about this sere, but such information as is available indicates clearly that it is very distinct from those already described. In some areas, e.g. Lough Ine, Skibbereen River, the marshes are undergoing considerable erosion, and no new marsh appears to be developing, so that it is more or less impossible to ascertain the primary stages. Another impediment to deduction is that the areas of marshland are much smaller than those around the English coast. The characteristic features of these marshes are:

(1) The soil is a form of marine peat although it is not so compact as that found in New England marshes. It differs very considerably from the soils of the seres already described, and is a further argument for the part played by soil in determining the general facies of the different seres.

(2) There is an abundance of marsh fucoids, especially forms of *Fucus spiralis*.

(3) The banks of the creeks commonly show a zonation of algae, a feature which can be associated with the relative resistance of peat to erosion. It would seem that the following lines of development are represented in this sere.



SUMMARY

A study of the succession to be observed on the salt marshes of Norfolk and the British Isles generally leads to the following conclusions.

1. The succession is by no means simple, that on the east coast being the most complex.

2. The salt marshes of the British Isles fall into four seres, those on the east coast, the south coast (probably including also the north coast of France), the west coast (including the west coast of Denmark) and the Irish coast.

3. The general vegetation of the seres is controlled primarily by the character of the soil, the east coast marshes possessing a more or less firm clay, the south coast a soft silt, the west coast much sand and the Irish marshes forming a kind of marine peat.

4. It is suggested that the succession should be regarded as dynamic because there is evidence that under suitable conditions there is a development to reed swamp and hence a woodland or other climatic climax is potentially possible.

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STUDIES IN THE ECOLOGY OF WICKEN FEN

IV. CROP-TAKING EXPERIMENTS

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(*With nineteen Figures in the Text*)

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A. Introduction—communities and methods

Of the great area of alkaline peat-land filling the landward half of the East Anglian fens, little has been spared conversion into arable ground. At Wicken Fen, 11 miles to the north-east of Cambridge, there is, however, one relict of the former natural fenland vegetation. Even this has remained by no means immune from interference, and ecological study of its plant communities has indicated control by many human activities of varying kind and intensity. It was suggested (Godwin, 1929) that the most widespread disturbance had been produced by a system of cutting the natural plant cover for thatch or for animal bedding. This cropping was usually at intervals of four or five years in the "sedge" communities that yielded a crop for thatch (*Cladieta* or more often *Cladio-Molinieta*), and at intervals of one or two years in the "litter" communities (*Molinieta*). These communities were not merely subject to this crop-taking: they had actually been produced by its agency. This was indicated by much circumstantial evidence, such as the straight boundaries which limit these communities and correspond to the edges of separate fen-holdings of the recent past: the records of recent "agricultural" treatment of the different areas, their disposition on the fen, and the absence of other factors, such as differing ground-level, all pointed in the same direction. The hypothesis was formulated that the "mixed-sedge" and "litter" communities were products of deflected successions induced by different intensities of crop-taking. Studies of water-level relationships in the fen (Godwin & Bharucha, 1932) later confirmed the view that neither *Molinieta* nor *Cladio-Molinieta* could have a place in the natural prisere of the fen.

Direct experimental proof of the effect of crop-cutting on the fen communities was not at that time forthcoming, but experiments begun in 1927 have now given data which supply this lack, and it is with these that the present paper is concerned.

In the summer of 1927 two areas, each 100 × 20 m., were enclosed by a post and wire fence. One strip lay in a uniform area of "mixed-sedge" in plots nos. 618 and 618*a* of Wicken Sedge Fen, and the other in a rather less uniform area of "litter" in plots nos. 580 and 581. Each strip was divided into five squares of 20 m. sides, and of these the first has been cut at intervals of 1 year the second every 2 years, the third every 3 years, the fourth every 4 years, and the fifth has been left uncut. The cutting was made in late October in conformity with fen practice, and after scything the crop was removed. At the outset of the experiment, in October 1927, all five squares were cropped.

The record of vegetational changes has been followed by three indices:

(i) a brief field description of the areas, first made in 1927 and repeated in 1940;

(ii) the mapping of a permanent 1 m. quadrat in each of the five squares of each strip;

(iii) analysis of the crop produced from each of the above metre-quadrats at the appropriate time of cutting.

Of these indices the last is the most interesting, since it gives the most continuous record, and, as might be expected, the changes are most striking in the area of "mixed-sedge" subjected to cutting every year.

B. FIELD NOTES ON CHANGES IN EXPERIMENTAL PLOTS

In order to demonstrate the nature of the two communities experimented upon, it will be convenient to reprint the two field records made when the experiment was first set up.

Cladio-Molinietum (see Fig. 1)

The *Cladium* is obviously dominant, reaching a general level of 1·2 m. The *Molinia*, which is less than 1 m. high, is probably equally abundant, but less conspicuous. Spikes of *Phragmites* growing 1·5–1·7 m. high are not very abundant; say an average of two or three per square metre. Spaced apart by distances of the order of 20 m. are clumps of bushes of *Rhamnus frangula* standing above the level of the *Cladium* and obviously left at the last cutting. Scattered seedlings of *Rhamnus frangula* are very abundant throughout the sedge, averaging 0·5 m. high, and at a very rough guess four or five to the square metre.

Eupatorium cannabinum occurs in local patches perhaps 10 m. apart. *Angelica silvestris, Peucedanum palustre, Lysimachia vulgaris* and *Hydrocotyle vulgaris* (in the *Molinia* tussocks) are less abundant than the *Eupatorium*.

Salix repens var. *fusca* is rather uncommon, e.g. one bush per 100 sq. m.

Molinietum (see Fig. 2)

The dominant plant is obviously *Molinia*, and on casual inspection there seems to be no *Cladium*, though a very few small patches do occur sporadically. *Phragmites* is more abundant than in the sedge and grows about 1·5 m. high—there are about ten living shoots per square metre. *Rhamnus frangula*, up to 0·5 m. high, is less abundant than in the sedge, 0–5 bushes per square metre (say an average of two); there are many isolated clumps 1·5–2 m. high, perhaps 10–20 bushes in each square of 20 m. sides. The south-west end has big clumps 2·5 m. high. *Salix repens* var. *fusca* occurs sixty or more to the 20 m. square. *Scabiosa succisa*, *Angelica silvestris*, *Thalictrum flavum*, *Cirsium anglicum*, *Hydrocotyle vulgaris*, *Valeriana dioica* and *Ulmaria palustris* are all fairly abundant, though irregularly distributed in patches, there being 10–20 patches of each plant in one 20 m. square. *Juncus obtusiflorus* is very abundant, its frequency being of the same order as that of *Phragmites*, though the plant is of very different habit. *Carex panicea* is equally abundant also, though more evident during its flowering period in spring, when its shoots are a glaucous green, than later in the season.

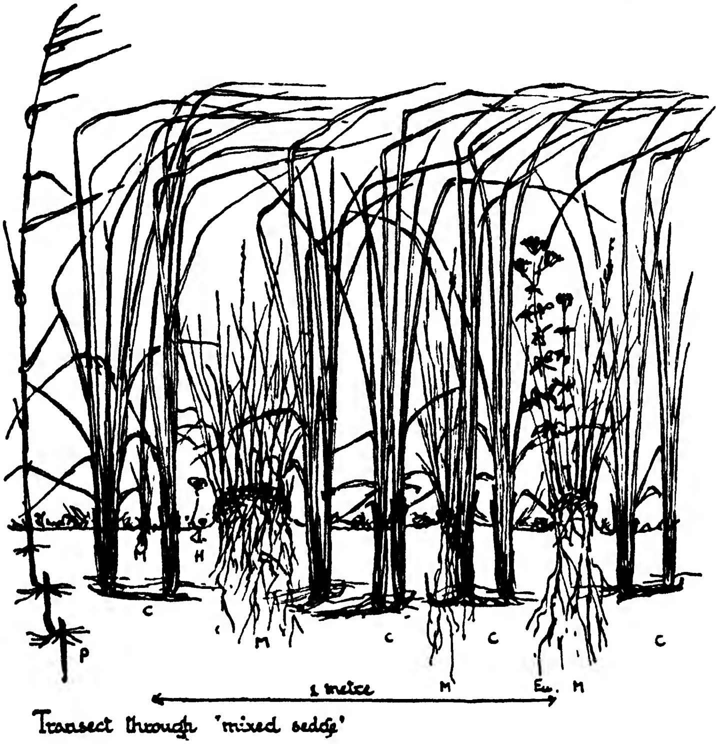

Fig. 1. Diagrammatic bisect through Cladio-Molinietum ("mixed-sedge") community. The general vegetation level is about 1·1 m. above soil-level, and is shown by the bent-over leaves of *Cladium mariscus* (*C*), through which project occasional shoots of *Phragmites communis* (*P*). Two small tussocks of *Molinia caerulea* (*M*) are shown, in one of which a plant of *Eupatorium cannabinum* is growing. One small plant of *Hydrocotyle vulgaris* (*H*) is shown, and on the ground surface is a discontinuous moss layer consisting chiefly of *Hypnum cuspidatum*. The mattress of dead leaves has not been shown, but it is very dense in the lower 40 cm. or so of the vegetation. (Reproduced by courtesy of Prof. J. S. Gardiner from *The Vegetation of Wicken Fen*, 1929.)

Thus the litter differs from "sedge" by the presence of *Juncus* and *Carex*, *Scabiosa* and *Valeriana*, the first two being in great abundance, by the relatively greater abundance of *Molinia*, *Salix* and *Phragmites*, and by the almost complete absence of *Cladium* and the infrequency of *Lysimachia*.

It will make comprehension of the data easier if we say at once that the most interesting result of the experiment is to demonstrate a clear turn-over of the Cladio-Molinietum towards Molinietum under the once yearly cropping, and less pronounced tendency but in the same direction under less frequent cropping. In Table 1 are given the frequencies of phanerogamic species in the five squares of the Cladio-Molinietum in 1940, together with comparable lists for the "mixed-sedge" and "litter" areas as they were when the experiment began.

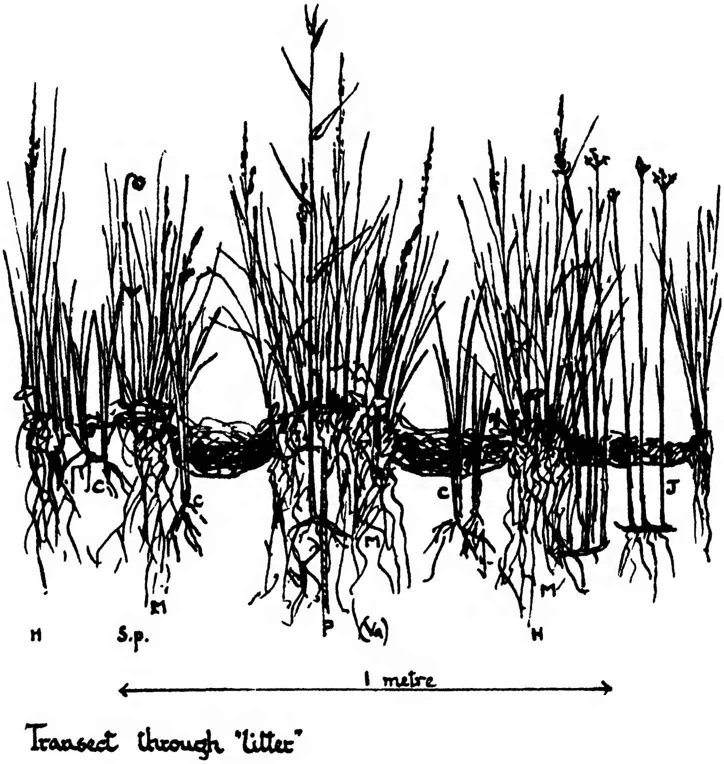

Fig. 2. Diagrammatic bisect through Molinietum ("litter") community. The general dominant is *Molinia caerulea* (*M*) rising to a general level of about 0·6 m. above soil level. Other species shown are *Juncus obtusiflorus* (*J*), *Carex panicea* (*C*), *Scabiosa succisa* (=*Succisa pratensis*) (*S.p.*), *Phragmites communis*, *Hydrocotyle vulgaris* (*H*). Seedlings of *Valeriana dioica* (*Va*), together with *Hypnum cuspidatum*, occur on the surface of the tussocks, and in the hollows the ground is covered with dead-leaf mattress. (Reproduced by courtesy of Prof. J. S. Gardiner from *The Vegetation of Wicken Fen*, 1929.)

It is apparent from this table that the vegetation in the square cut each year has taken on most of the characteristics of the "litter". *Cladium* is very dwarf and less frequent, *Molinia* is dominant, *Carex panicea* and *Juncus obtusiflorus* are abundant, and the characteristic species, *Cirsium anglicum*, *Valeriana dioica*, *Thalictrum flavum*, *Scabiosa succisa* and *Orchis incarnata* are present though not yet quite so abundantly as in mature Molinietum. Moreover, the columns of five different cutting intensities show a progressive series in their vegetational composition. The first three species, which are all characteristic of "sedge", show progressive diminution with increasing cutting frequency. *Cladium mariscus* is a tall evergreen plant, the leaves of which last about 3 years (Conway, 1936), and yearly cutting injures it severely. Both *Eupatorium cannabinum* and *Peucedanum palustre*, it will be noted, are tall species, and this may well relate to their ability to live along with *Cladium*.

Table 1. *Changes in Cladio-Molinietum from* 1927 *to* 1940

		"Mixed sedge"	Frequencies in 1940 after being cut at intervals of years					"Litter"
			Uncut	4	3	2	1	
1	Cladium mariscus	d.	d. (tall)	d. (tall)	co.–d.	a.	f.–a. (dwarf)	—
2	Eupatorium cannabinum	f.	f. (flg.)	f. (flg.)	f. (flg.)	o.	o. (seedling)	—
3	Peucedanum palustre	f.	f. (flg.)	r. (flg.)	o.	r.	—	o. (seedling)
4	Lythrum salicaria	o.	o.	o.	o.	o.	o.	—
5	Lysimachia vulgaris	o.	o.	o.	o.	—	r.	r.
6	Salix repens var. fusca	o.–f.	f.	o.	o.	o.–f.	o.	o.–f.
7	Angelica sylvestris	o.	r.	—	—	—	o.	f.
8	Molinia caerulea	a	a.	s –d.	co.–d.	d.	d.	d.
9	Hydrocotyle vulgaris	o.	l.f.–r.	f.	f.–a.	a.	a.	a.
10	Phragmites communis	f.	f.	f.	f.	f.	a.	a.
11	Juncus obtusiflorus	r.	r.	l.f.	l.f.	f.	l.a.	a.
12	Carex panicea	r.	—	—	l.f.	l.f.	a.	a.
13	Cirsium anglicum	—	—	r.	r.	? r.	o.	f.
14	Valeriana dioica	—	—	—	r.	—	l.f.	f.–a.
15	Thalictrum flavum	—	—	—	—	o.	o.	f.
16	Scabiosa succisa	r.	—	—	—	—	o.	f.
17	Orchis incarnata	—	—	—	—	—	o.	o.

The reason for their susceptibility to cutting is not apparent. Species nos. 4–7 are not particularly more characteristic of "mixed-sedge" than of "litter": they are species of moderate height. Species nos. 8–10, although present both in "mixed-sedge" and in "litter", are more abundant in the latter and through the series increase when cutting intensity is greatest. *Molinia* and *Phragmites* both produce annual green shoots and should suffer little by removal of the dead shoots in autumn. They may both be expected to benefit by the removal of competition of *Cladium*, and this applies particularly to the dwarf *Hydrocotyle vulgaris*. The remaining species (nos. 11–17) are rare or absent in the "mixed-sedge", but have entered and spread to different degrees in the cropped areas. *Juncus obtusiflorus*, *Carex panicea*, and *Valeriana dioica* have become increasingly abundant with increasingly frequent cutting, and give a very characteristic aspect to the vegetation of the square cut each year. This last group of seven species is composed entirely of dwarfer forms, whose chief photosynthetic regions are within a few inches of the ground, and it is evidently only the removal of competition of the taller *Cladium* which has permitted their establishment and extension. It is possible that to this last group might be added *Mentha aquatica*, which has appeared locally in the area cut each year.

Seedling bushes (mostly *Frangula alnus*) have not been mentioned in the frequency table, for they occur freely in all the squares. Only in the uncut area, of course, do tall bushes develop and play an important role in the community. These bushes are naturally even more susceptible to cutting than the *Cladium* itself, and it is their suppression which permits both *Cladio-Molinieta* and *Molinieta* to develop on the fen.

It is unfortunate that the five areas of "litter" vegetation set aside in 1927 for different cutting treatments were not initially fully comparable. Squares nos. 1, 2 and 3 were uniform, but no. 4 had more residual *Cladium* in it, and no. 5 a considerable amount. This was because cutting had been more frequent in the first three. The vegetation in squares nos. 4 and 5 was therefore initially of a type between Molinietum and Cladio-Molinietum, square no. 5 being most removed from the "litter" type. Thus although changes are evident which suggest reversion to Cladio-Molinietum with the longer intervals of cutting, it will be safer to disregard such indications in the table of field notes on composition of the vegetation of the five squares in 1940.

Table 2. *Field lists of Molinietum areas, August* 1940

	Cut at intervals in years of				
	1 (no. 1)	2 (no. 2)	3 (no. 3)	4 (no. 4)	Uncut (no. 5)
Cladium mariscus	r.	l.	—	l.a.	v.a.
Eupatorium cannabinum	r.	r.	—	—	—
Peucedanum palustre	o.	f.	o. (flg.)	f. (tall, flg.)	f.
Lythrum salicaria	o.	o.	f.	o.–f. (flg.)	f.
Lysimachia vulgaris	o.–f. (not flg.)	—	o. (flg.)	o.–f. (flg.)	f. (not flg.)
Salix repens, var. fusca	o.	o.	—	o.–f.	f.–a. (tall)
Angelica sylvestris	o.	—	—	r.	—
Molinia caerulea	d.	d. (taller)	d. (taller)	d.	sub. d.
Hydrocotyle vulgaris	a.–v.a.	a.	a. (less)	a.	f.
Phragmites communis	a. (dwarf)	a. (taller)	a. (taller)	a. (v. tall)	a.
Juncus obtusiflorus	v.a.	v.a.	a.	a.	l.a.
Carex panicea	v.a.	v.a.	a.	f.–a.	—
Cirsium anglicum	f.–a. (flg.)	o.–f. (flg.)	o. (flg.)	—	—
Valeriana dioica	a.	a.	a.	o.–f.	—
Thalictrum flavum	o.	o.	r.	o.	r.
Scabiosa succisa	f.–a. (flg.)	a. (flg.)	f. (flg.)	o.–f. (flg.)	—
Orchis incarnata	o.	—	—	—	—
Mentha aquatica	o.	—	—	—	—
Ulmaria palustris	f.	o.	r.	—	o.
Symphytum officinale	—	—	r.	o.	—
Calamapostis lanceolata	o.–l.f.	—	o.	f.	—
Potentilla erecta	—	o.	r.	—	—
Galium palustre	—	—	—	r.	—
Galium uliginosum	—	r.	—	—	—
Lathyrus palustris	—	o.	r.	o.	o.–f.
Iris pseudacorus	—	—	—	r.	—
Valeriana officinalis	r.	—	—	—	—
Cirsium palustre	o.	—	—	—	—

If we consider only the first three columns, however, we can still see evidence of changes following varying frequency of crop-taking. As this decreases, (i) the dominant *Molinia* and also *Phragmites* become taller, (ii) *Juncus obtusiflorus, Carex panicea, Scabiosa succisa, Cirsium anglicum*, and *Hydrocotyle* *vulgaris* become less abundant. It is very striking that the species which we regard as especially typical of Molinietum should thus show diminution in frequency when cut at intervals increasingly longer than 1 year. The absence of *Mentha aquatica* and *Orchis incarnata* in all save square no. 1 is consonant with the other changes, but in species of such low frequency chance may be responsible for this effect.

It should be noted that the species list (which excludes bushes other than *Salix repens* var. *fusca*) is longer in the area cut each year than in those cut at 2- or 3-yearly intervals.

C. REMAPPING OF METRE-QUADRATS

Although there are nine permanent metre-quadrats in the experimental areas, it will suffice here to consider the results of remapping only four of them, which represent however the range of changes observed. All nine quadrats are dealt with in the section on crop analyses.

(i) *Quadrat VI, "mixed-sedge" cut every year for* 12 *years* (Fig. 3). Very pronounced changes are apparent. The *Cladium* shoots have diminished very greatly in number, from ninety-four in 1927 and seventy-nine in 1932, to thirty in 1940: the length, width and number of the sedge leaves are also reduced, so that many shoots are no bigger than those of *Carex panicea.* On the other hand the tussocks of *Molinia* have increased very greatly in area, and although some of the tussocks are now dying in the middle, seedlings are frequent. Many shoots of *Carex panicea* had appeared in 1932, and they were very abundant in 1940. *Juncus obtusiflorus* had not yet in 1940 appeared in the quadrat, although present in many other parts of the experimental area. *Hydrocotyle* appeared in 1932 and there are several shoots present in 1940. *Phragmites* shoots increased in number from nine in 1927, and nineteen in 1932, to thirty-eight in 1940, but the shoots became smaller, and apparently two or three axilliary shoots had often replaced a single large shoot from the same persistent vertical rhizome. Moss covering became more general as the yearly cutting continued, but only in parts when the ground was free from a cover of dead leaves. One seedling of *Mentha aquatica* had appeared in 1940. All these changes represent the entry and extension of species typical of "litter" vegetation, consequent on the severe regression of *Cladium* caused by the yearly cutting. *Eupatorium cannabinum* still remains in the quadrat in 1940.

(ii) *Quadrat VIII, "mixed-sedge" cut every* 3 *years for* 12 *years* (Fig. 4). The changes between 1927, when the quadrat was first mapped, and 1940, are as follows. There has been considerable extension of *Molinia* tussocks, and the establishment in small amount of *Carex panicea,* which however is not flourishing. *Phragmites* shoots have increased in number, and seedlings of

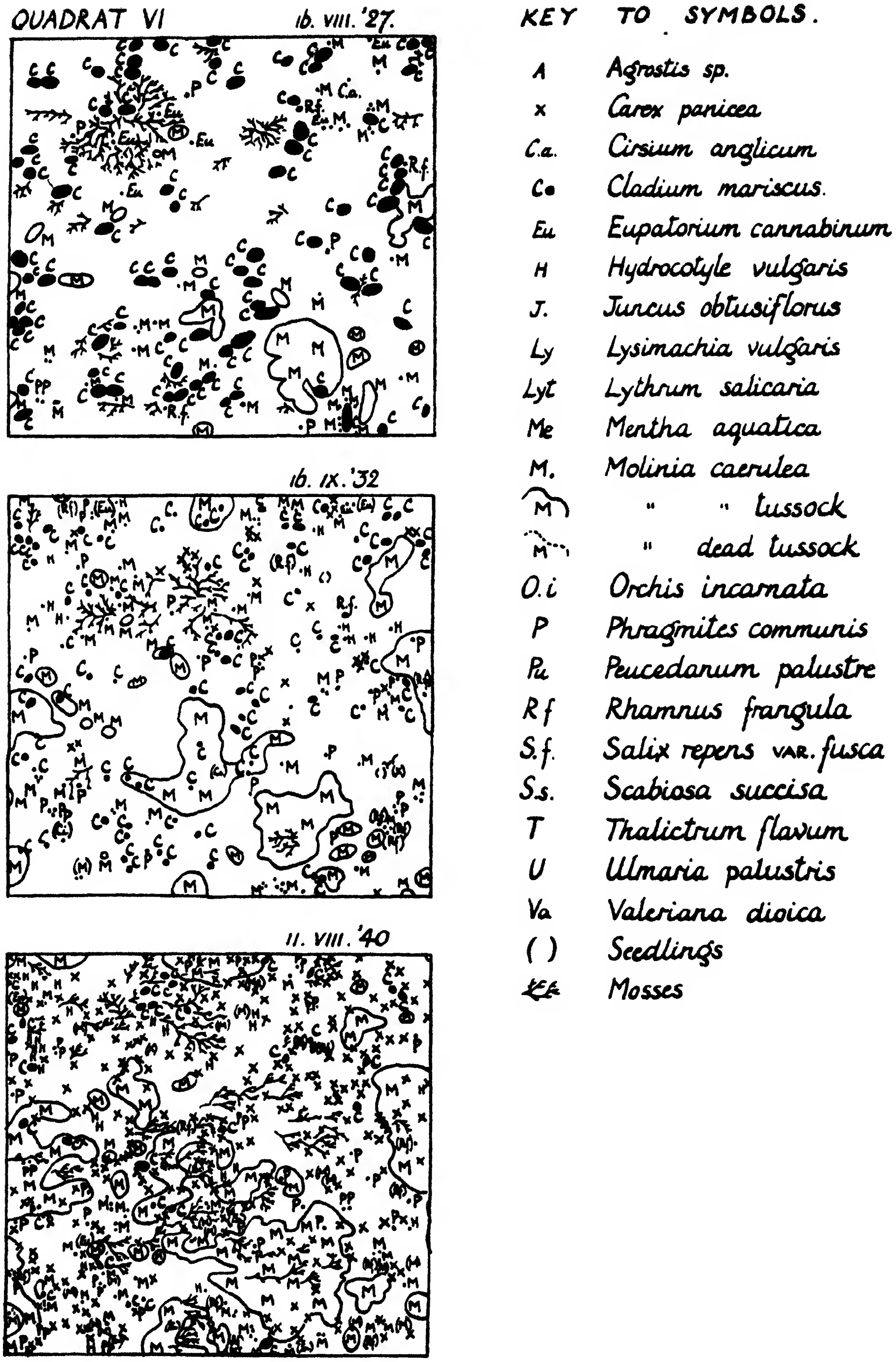

Fig. 3. Permanent metre-quadrat (VI), in Cladio-Molinietum, cut every year in late October from 1927, and mapped in 1927, 1932, 1940. The key to symbols applies to Figs. 3–6. Note the diminution in *Cladium*, extension of *Molinia* and *Phragmites*, appearance and spread of *Carex panicea*, all indicative of change towards Molinietum.

Mentha aquatica and *Orchis incarnata* are present, although, since the map was made less than 1 year after a crop, these species will not necessarily persist. All the above features suggest a tendency to move slowly towards the character of "litter", but the diminution in severity of *Cladium* dominance cannot be large, for diminished vigour in the shoots of this species is accompanied by an increase in their number from sixty-four to seventy-seven. Perhaps this increase follows the lessened competition of shoots of this species with one another.

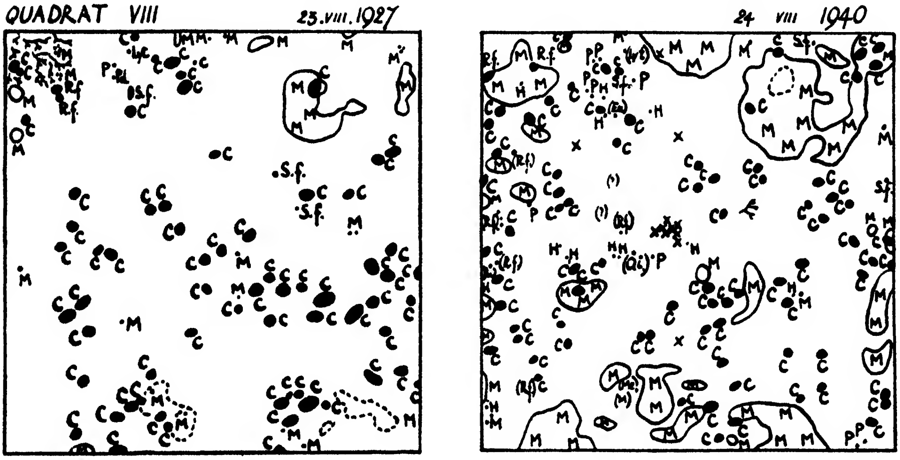

Fig. 4. Permanent metre-quadrat VIII, in Cladio-Molinietum cut at 3-year intervals since 1927, and mapped in 1927 and 1940. Note the slowness of change towards Molinietum: although *Molinia* has extended, *Cladium* has only diminished slightly and *Carex panicea* though present is small in amount. Symbols as in Fig. 3.

(iii) *Quadrat I, "litter" cut every year for* 12 *years* (Fig. 5). In comparison with the frequently-cropped areas in *Cladio-Molinieta* those in *Molinieta* subject to frequent cutting show very little change. The outlines of *Molinia* tussocks are very difficult to map accurately, but nevertheless they must have extended considerably between 1927 and 1940. These tussocks at one time were tall with steep sides (as now in quadrat XII), but now the clefts between are filling in and producing gentle slopes and indefinite margins. *Carex panicea* and *Juncus obtusiflorus* have been both maintained, the former growing indifferently through *Molinia* tussocks and between them, the latter mostly between them as if unable to penetrate the tough mass. *Scabiosa succisa* plants have persisted and enlarged and there are numerous seedlings. A few *Valeriana dioica* plants and some seedlings have been present throughout the experimental period. There has been little or no *Hydrocotyle vulgaris*, and *Orchis incarnata* has come in and disappeared again. *Phragmites communis* shoots have increased, 9 → 8 → 20 → 36.

The *Phragmites* and *Molinia* thus show progressive change in amount, but the essential "litter" character of the community is unaltered, and this indeed is what would be expected if litter is, as we suppose, itself produced by repeated yearly cutting.

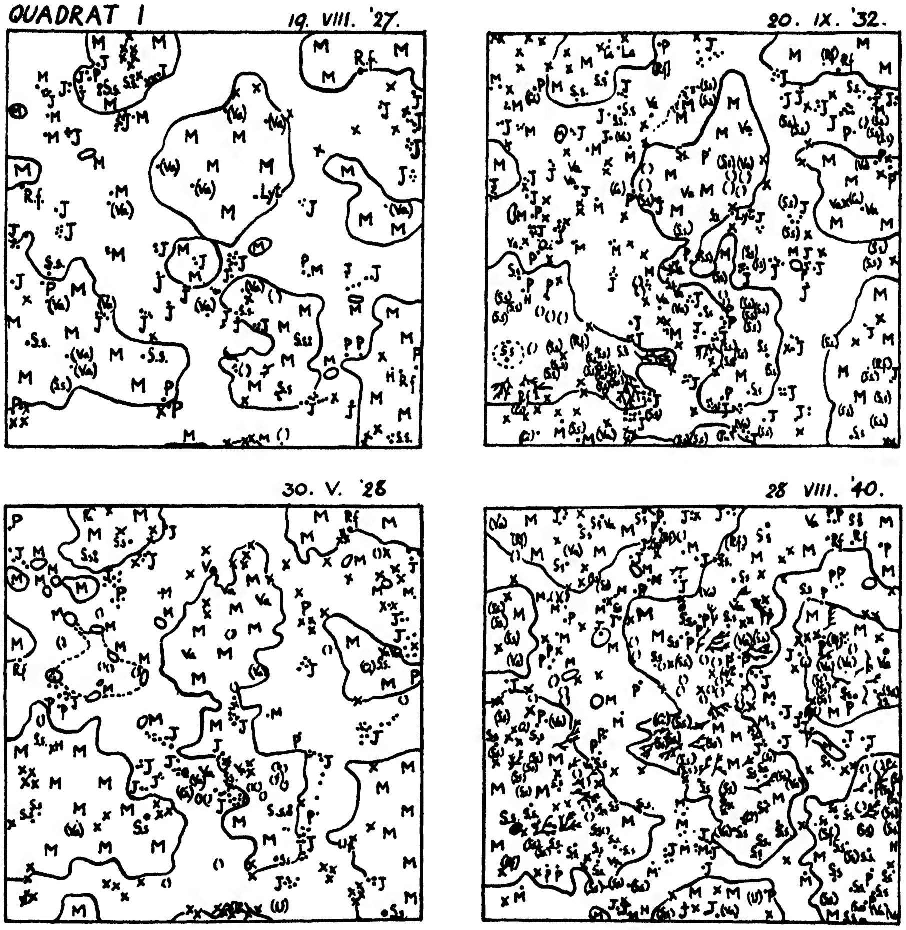

Fig. 5. Permanent metre-quadrat I, in Molinietum cut every year from 1927, and mapped in 1927, 1928, 1932 and 1940. Apart from extension of *Molinia* and *Phragmites* the community has altered little under this cutting treatment. Symbols as in Fig. 3.

(iv) *Quadrat XII, suspension of cropping for* 22 *years in "mixed-sedge"-"litter"* (Fig. 6). Quadrat XII is situated in plot no. 618. Although this plot has the general characteristics of Cladio-Molinietum, it had been cut during the Great War of 1914–18 at close intervals of time, and had developed some of the characteristics of Molinietum. When it was set aside as a reserve for successional studies in 1923 it contained only seedling bushes (apart from the margins), and the herbaceous vegetation still had signs of clear progression towards a "litter" (Molinietum) type. Thus it will be noticed (Fig. 6) that much *Carex panicea* was present in quadrat XII when Prof. Wadham first mapped it in 1923. The quadrat has been remapped three times subsequently, in 1927, 1932 and 1940. On each occasion this has meant trampling round the square and removal of the dense accumulation of the "mattress" of dead

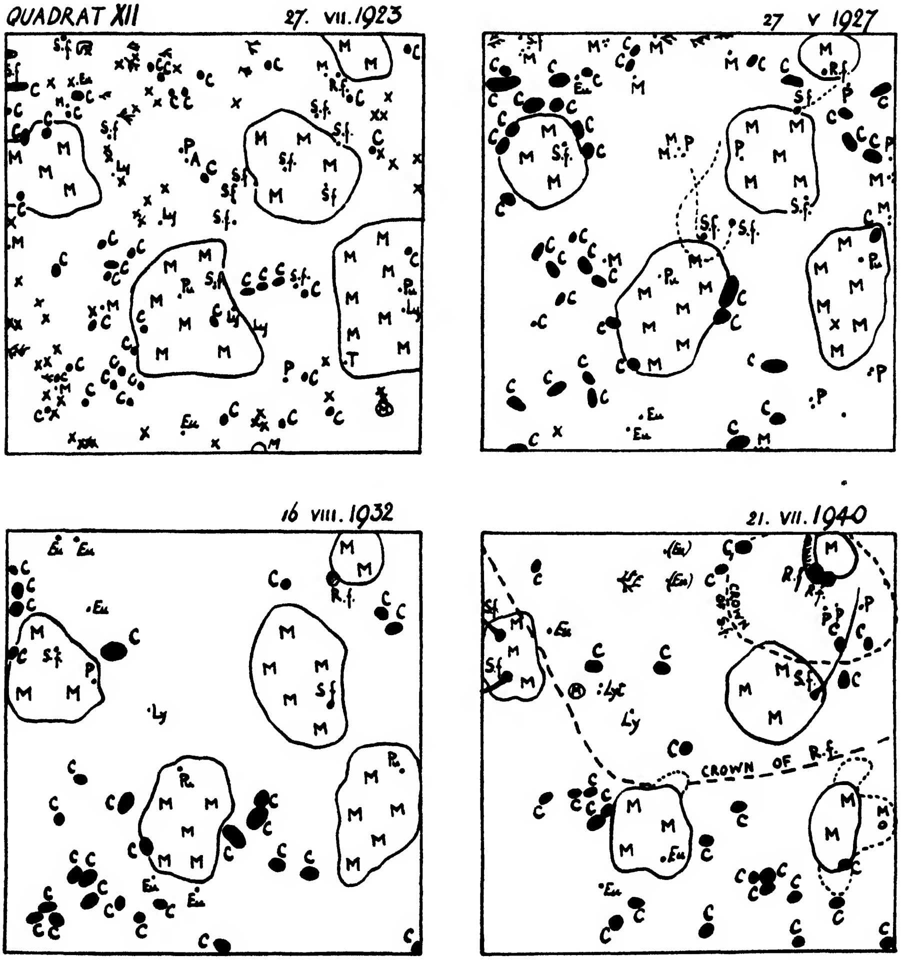

Fig. 6. Permanent metre-quadrat XII, in a community transitional between Cladio-Molinietum and Molinietum, left uncut since about 1918, and remapped in 1923, 1927, 1932 and 1940. Although the *number* of *Cladium* shoots has diminished they are more vigorous and persistent so that the dominance of this species has increased. *Molinia* has diminished and *Carex panicea, Thalictrum flavum* and *Peucedanum palustre* have disappeared. There is a general tendency to move from the character of Molinietum back towards that of Cladio-Molinietum. Symbols as in Fig. 3.

leaves which is so striking and important a feature of *Cladium*-dominated communities. This mattress was restored as far as possible after each mapping.

The changes during the period can be seen by comparison of the four quadrat maps. The principal changes will be recognized as the following:

(i) Forty-nine shoots of *Carex panicea* present in 1923 had diminished to one in 1927 and the plant has since been absent; (ii) *Thalictrum flavum* disappeared in 1927; and (iii) *Peucedanum palustre* between 1932 and 1940; (iv) *Lythrum salicaria* was tall and healthy until 1932, but by 1940 was represented only by unhealthy etiolated shoots; (v) *Molinia caerulea* itself had living tussocks covering 25% of the quadrat area in 1923 and there were also many separate small plants, but by 1932 none of the isolated plants remained and the live tussock area had by 1940 diminished to 13% of the quadrat area. The tussocks had grown much taller (20–25 cm.) but their margins were evidently dying; (vi) *Eupatorium cannabinum* continued tall and healthy till 1932: it persists less flourishing in 1940, but two first-year seedlings are present as well as shoots from the old subterranean stocks; (vii) several shoots of *Salix repens* var. *fusca* died out between 1923 and 1932, but in 1940 there remained two very substantial bushes of this plant, one with its crown 1 m. high within the quadrat; (viii) *Cladium mariscus*, the sedge plant itself, shows a diminution of number of living shoots in the quadrat of 43 → 39 → 28 → 27, but the shoots are now much larger than they were (now *c.* 2 m. long), and persisting erect dry dead leaves contribute abundantly to the "mattress" in the quadrat; (ix) the seedling of *Frangula alnus* (*Rhamnus frangula*) present in 1923 has in 1940 become a bush 2·5 m. tall which has a crown extending over half the quadrat, and immediately outside the quadrat in 1940 the first bare areas due to the bushes' shade carried a few seedlings of the same species.

The above changes constitute a regular pattern of progressive alteration. They represent in fact a secondary succession following removal of the deflecting factor of crop-cutting. This effectively operates by reassumption of dominance of *Cladium mariscus*, but by 1940 it can be seen that this itself is bound soon to be overtaken by the increasing dominance of *Rhamnus frangula* bushes as they extend and coalesce to form fen scrub (carr) over the area. With the increasing dominance of *Cladium* we witness the disappearance or retrogression of the typical species of "litter" vegetation. *Carex panicea*, *Molinia* and *Thalictrum flavum* show it clearly: species of intermediate status such as *Peucedanum palustre* and *Lythrum salicaria* are eliminated slowly. The sedge itself seems to show signs of internal competition between its own shoots as the numbers decrease, and the species typical of Cladietum or Cladio-Molinietum, i.e. *Eupatorium cannabinum* and *Salix repens* var. *fusca*, persist.

D. DRY WEIGHT OF SORTED CROPS FROM METRE-QUADRATS

Each year, on 27 October, or within a day or two of this date, each metre-quadrat due for cutting was cropped by garden-shears, just above ground-level, where the scythe normally cuts. The crop was taken to the laboratory and there spread out near warm pipes to air-dry for three months. This gave a quite sufficiently accurate dry-weight basis for the big changes investigated in the experiment. Before weighing, the crop was sorted into component species: the bulk was made up by monocotyledons, and the fractions composed of twigs, herbs and mosses, and unsorted residue, although separately weighed, were always an insignificant part of the total and will not be further mentioned.

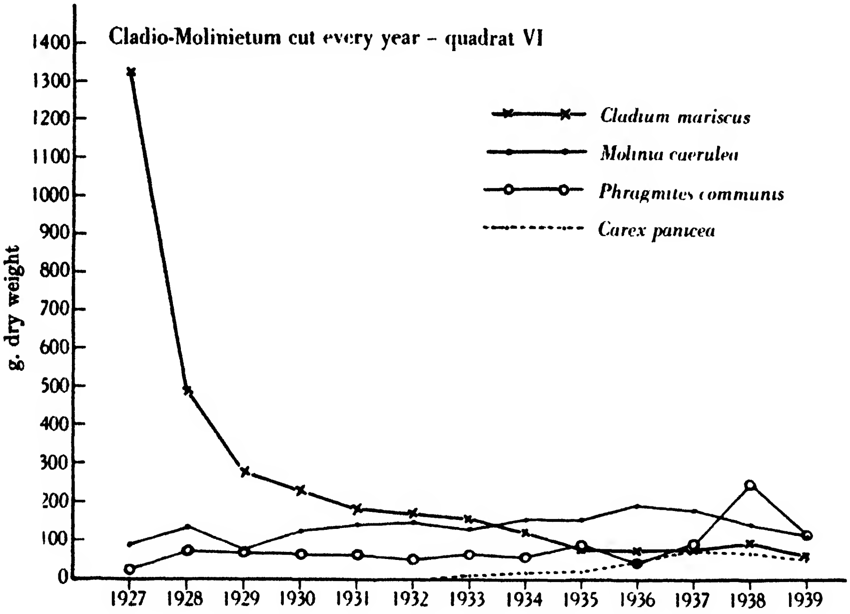

Fig. 7. Dry weights of the different components of the sorted crop from quadrat VI, in Cladio-Molinietum, taken in late October each year from 1927 onwards. The 1927 crop represents several seasons' growth, but subsequent crops contain one year's growth only. Note especially the great reduction of *Cladium mariscus*, the initial dominant, the entry and extension of *Carex panicea* and the general move towards the composition of a Molinietum crop.

(i) *Quadrats in Cladio-Molinietum.* The effects of yearly cutting upon "mixed-sedge" vegetation are very clearly brought out by the successive analyses of quadrat VI (Fig. 7). This shows above all the bad effect of yearly cutting on *Cladium mariscus* itself. The 1927 crop is exceptional in that, as the first crop, it includes leaves several years old, both living and dead. All subsequent values, however, record for the single year's growth a progressive diminution, so that the dominant species, which gave 70% of the dry-weight yield in 1928, 11 years later gave only 18%, which is less than the yield of *Molinia* or *Phragmites*, and only little more than that of *Carex panicea*. It is no doubt the evergreen habit of the sedge plant which makes it so susceptible to cutting, and in Scandinavia repeated and frequent cutting is recognized as the best means of eradicating this plant from reclaimed fenland. The importance of the interval between the crops is shown in Fig. 8, from which it is apparent that cutting every 2 years reduces *Cladium* slowly, cutting every 3 years has a small adverse effect, and cutting at 4-yearly intervals causes no reduction in the species under the conditions here involved. This agrees with the fact that "mixed-sedge" vegetation, cut by the fen-men at intervals of 3 or 4 years, appears to maintain its dominant to co-dominant *Cladium* for a long period of time.

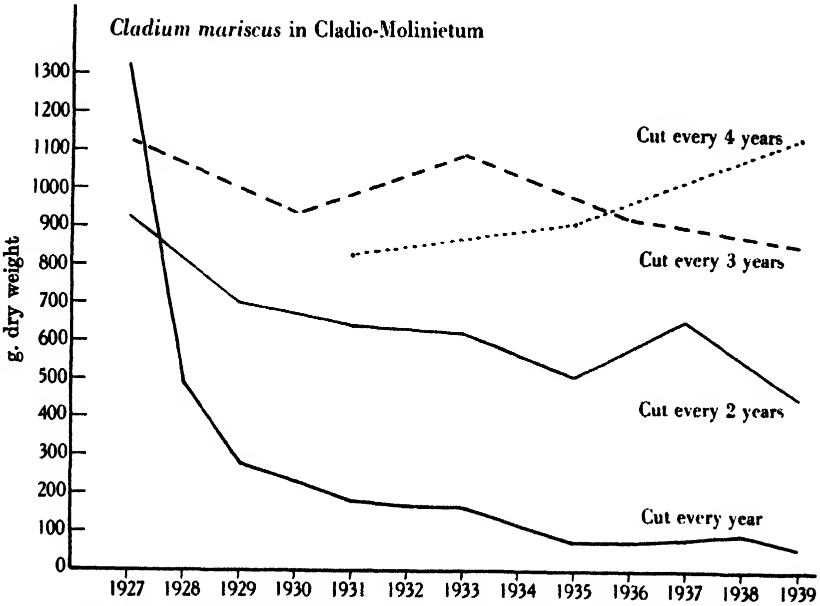

Fig. 8. Dry weights of *Cladium* produced in permanent metre-quadrats VI, VII, VIII and IX, in Cladio-Molinietum cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. Under yearly cropping *Cladium* diminishes rapidly, less rapidly as the interval lengthens, and the crop increases under 4-yearly cutting.

Further consideration of the analyses of quadrat VI (Fig. 7) shows that, from 1927 onwards, both *Molinia* and *Phragmites* have increased substantially in amount, and *Carex panicea*, first weighed in the 1933 crop, has increased to 14% of the dry weight in 1939. The composition of the 1939 crop, apart from the residual *Cladium*, is beginning to approximate to that of quadrats in the Molinietum (see table opposite).

	% of total dry wt. of year's crop					
	Cladium	*Molinia*	*Phragmites*	*C. panicea*	*J. obtusiflorus*	"Rest"
Quadrat VI, 1939 (Cladio-Molinietum cut each year)	18	33	34	14	—	1
Quadrat I, 1939 (Molinietum cut each year)	—	51	28	10	7	4

The effect of cutting Cladio-Molinietum at 2-year intervals is shown in quadrat VII (Fig. 9) from which it is apparent that a gradual decline in *Cladium* is accompanied by increases in *Molinia* and *Phragmites* and the entry and slight increase of *Carex panicea*. All these changes are in the direction of Molinietum, but the rate of change is very much less than that produced by yearly cutting. Fig. 10 shows that in quadrat VIII, cut every 3 years, changes of a similar kind are represented only by *Cladium* and *Molinia*, whilst the former remains much the largest component of the crop. The three analyses of the crops taken at 4-year intervals from quadrat IX seem to show no drift at all towards the character of Molinietum (Fig. 11).

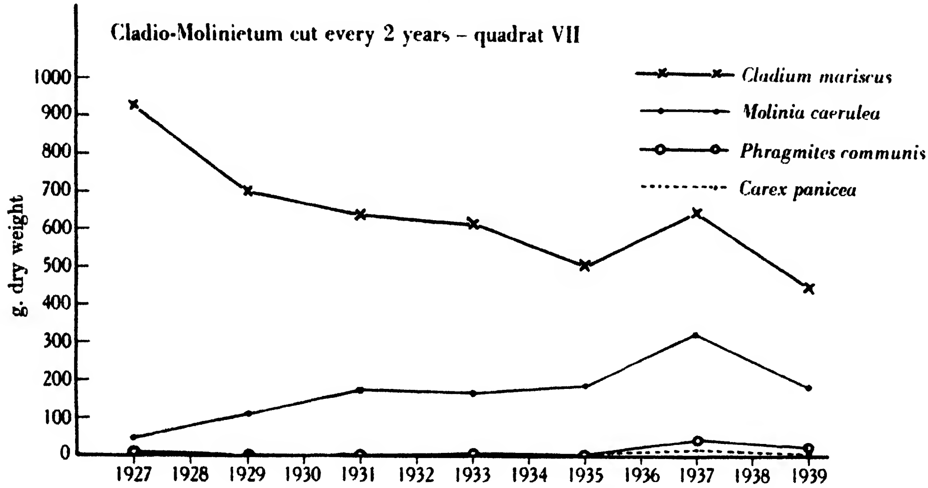

Fig. 9. Dry weights of the different components of the sorted crop from quadrat VII, in Cladio-Molinietum, cut at 2-year intervals since 1927.

(ii) *Quadrats in Molinietum.* In contrast with the effect upon Cladio-Molinietum, cutting, even every year, has not appreciably altered the composition of any of the quadrats in the Molinietum. This is clearly shown in quadrat I (Fig. 12). The data for the three quadrats cut at longer intervals have not been graphed, but can be recovered from the graphs for individual species given below.

(iii) *Individual species.* Consideration of the results of quadrat crop analyses, species by species, allows the recognition of such consistent systems of behaviour as exist in the relation of the species either to different frequency

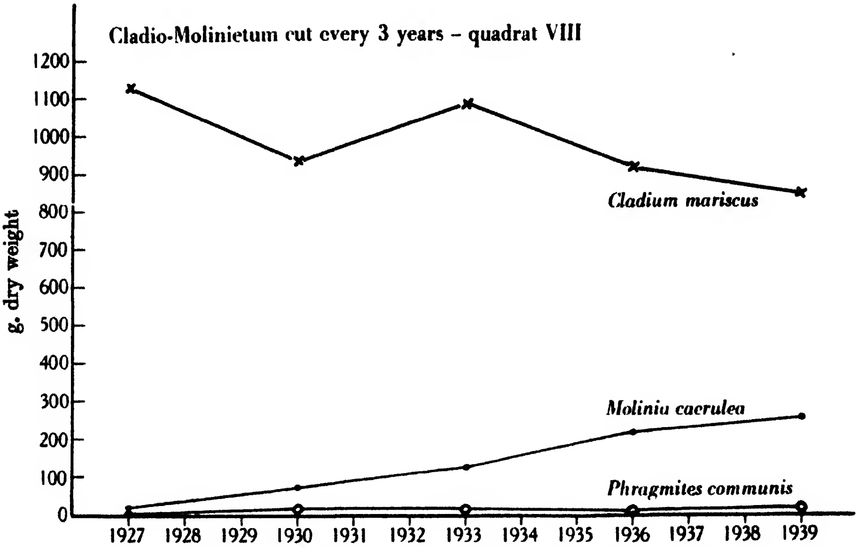

Fig. 10. Dry weights of the different components of the sorted crop from quadrat VIII, in Cladio-Molinietum, cut at 3-year intervals since 1927.

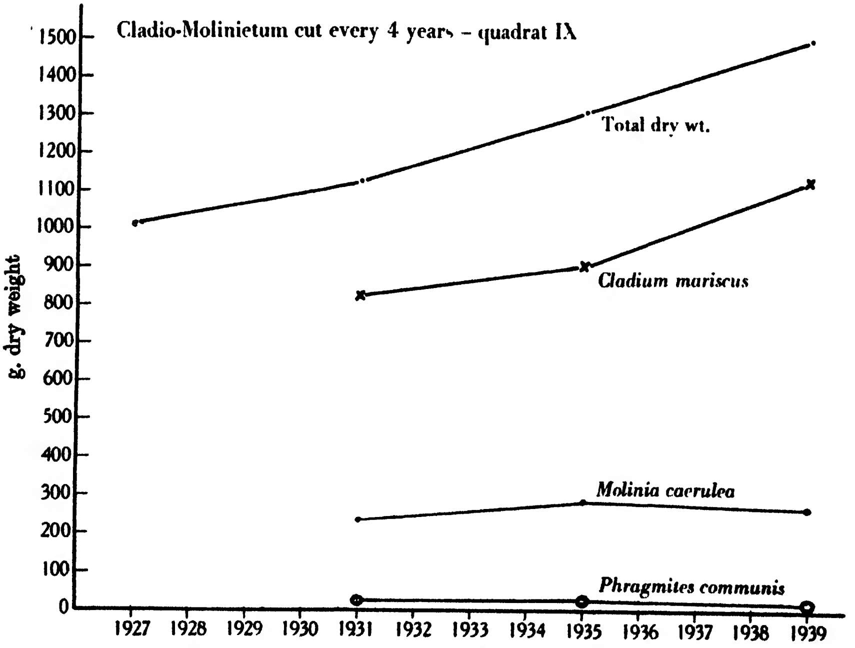

Fig. 11. Dry weights of the different components of the sorted crop from quadrat IX, in Cladio-Molinietum, cut at 4-year intervals since 1927.

of cutting, or to external factors such as climate. Before proceeding to such a consideration, however, it will be advantageous to point out some primary features of the species concerned, as we should expect them to stand in relation to major ecological factors. They are summarized below.

			Probable susceptibility to		
	Tallness of vegetative shoots (*ca.*) m.	Duration of shoots or leaves	Competition from the four other species	Cropping	Summer dryness
Phragmites communis	1·5	Annual	? Low	—	More
Cladium mariscus	1·2	Perennial leaves last 3 years	Low	High	More
Molinia caerulea	0·3	Annual	Moderate	Low	Less
Carex panicea	0·15	Short-lived, wintergreen	High	Low	More
Juncus obtusiflorus	0·4	? Wintergreen	? Moderate to high	—	Less

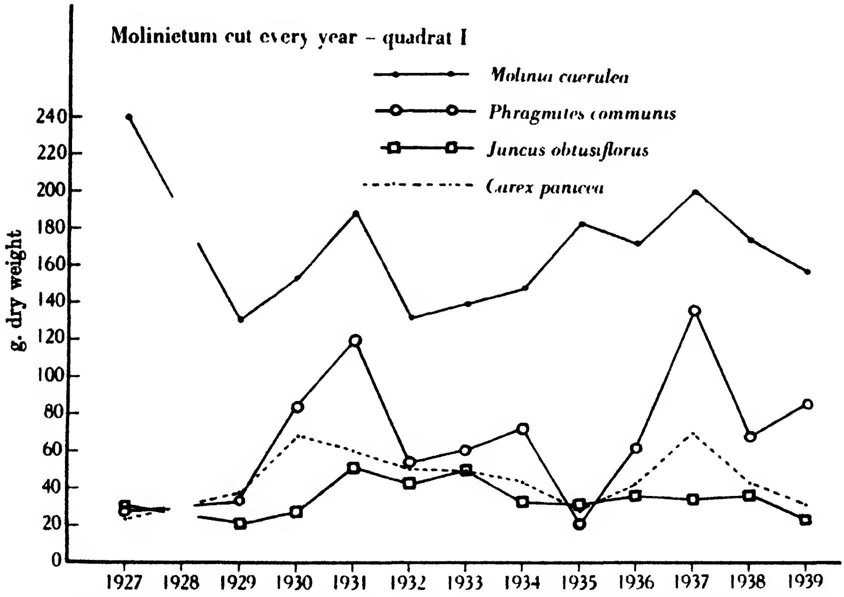

Fig. 12. Dry weights of the different components of the sorted crop from quadrat I, in Molinietum, cut every year since 1927. The composition has not appreciably altered during the experimental period.

The crop analyses applied to *Cladium* have already shown (Fig. 8) the susceptibility of this plant to cropping, and it need only be added that the irregularities in drift of the curves suggest that 1933 (and possibly 1937) was favourable to *Cladium*, and 1935 unfavourable. It will be recalled that Conway (1938) showed 1935 to have been much too dry in the summer for good growth of this species, which she describes as needing fully waterlogged soil for optimal growth. She also pointed out the damaging effect of the severe mid-May frosts of that year upon the shoots of *Cladium*.

Since the shoots of *Molinia* are annual (the food being transferred to swollen stem-bases in the autumn), each crop represents only one season's growth no matter how long the interval from the previous crop. In Molinietum (Fig. 13) the crop is heavy and gives no clear evidence of general drift, although 1931 and 1937 seem to have been years of high yield, and 1929 and 1930 of low. In Cladio-Molinietum (Fig. 14) the *Molinia* has increased under all degrees of cutting intensity, suggesting strongly that the plant is unharmed by winter cropping. It seems probable that only the constant maintenance of dense *Cladium* cover can repress *Molinia* under the conditions present at Wicken: even under 3-yearly cutting the *Molinia* crop has rapidly increased towards the values found in pure Molinieta. The figures suggest that 1936 and 1937 must have been favourable to this species and 1929 unfavourable.

When we compare the crop yields of *Phragmites communis* in Cladio-Molinietum (Fig. 15) with those in Molinietum (Fig. 16) the higher values in the latter are apparent. The yields in Cladio-Molinietum show rising values under cutting at 2-year and 1-year intervals, so that the possibility suggests itself that the heavier *Phragmites* crop is in some way produced by the frequent cutting: this is most likely due to the removal of the severe dominance of *Cladium*, which is still important although the heads of the *Phragmites* shoots project from the general level of the *Cladium* crop. Where shoots are so large and so few to the square metre, the accidents of occurrence inside or outside a given quadrat must lead to big irregularities in crop-yield, but the fluctuations are so large in the two sets of curves considered here that big seasonal effects must also be present. Thus 1931, 1937 (and possibly 1938) were favourable seasons, and 1935 and 1936 unfavourable.

Carex panicea in Cladio-Molinietum (Fig. 17) shows very clearly the same response to cropping already brought out by the field descriptions and quadrat maps: it barely alters under cropping every 3 years, increases slowly under 2-year cropping and rapidly under yearly cropping. It is thus clear how sensitive this plant must be to the competition of taller species. The crops from Molinietum (Fig. 18) show strikingly large variations from year to year, which can only reflect the operation of favourable or unfavourable seasons. 1930 and 1931 produced very high yields, and 1937 was also favourable, whilst 1935 and 1939 were unfavourable. It must, however, be remembered that in a species so sensitive to competition as this, a seasonal effect might operate through an effect on the dominant species rather than directly on *Carex panicea* itself, and it is possible that the high values in 1930 and 1931 are related to the bad seasons for *Molinia* in 1929 and 1930. These huge variations from one season to another deserve recognition in studies of the statistics of species frequency in plant communities.

Crop analyses for *Juncus obtusiflorus* (Fig. 19) are restricted to quadrats

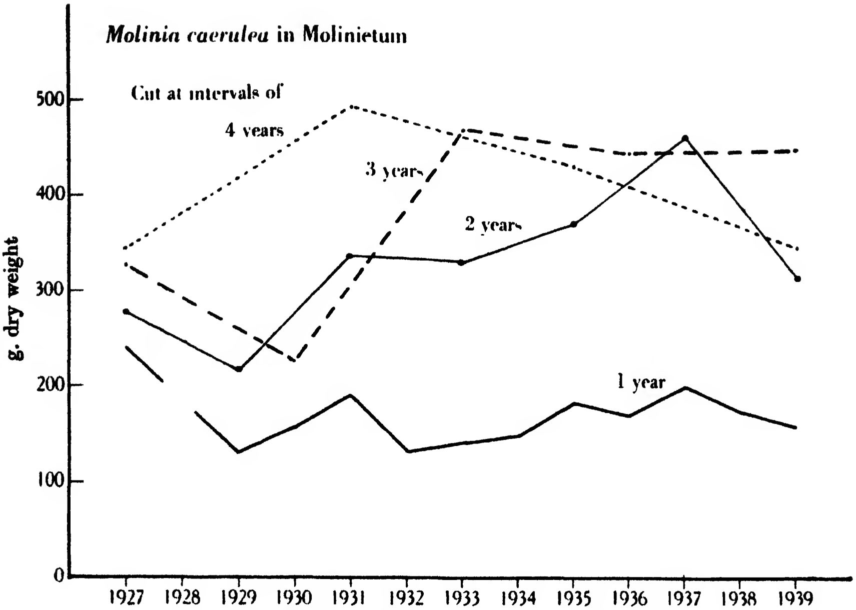

Fig. 13. Dry weights of *Molinia* produced in permanent metre-quadrats I, II, III and IV, in Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927.

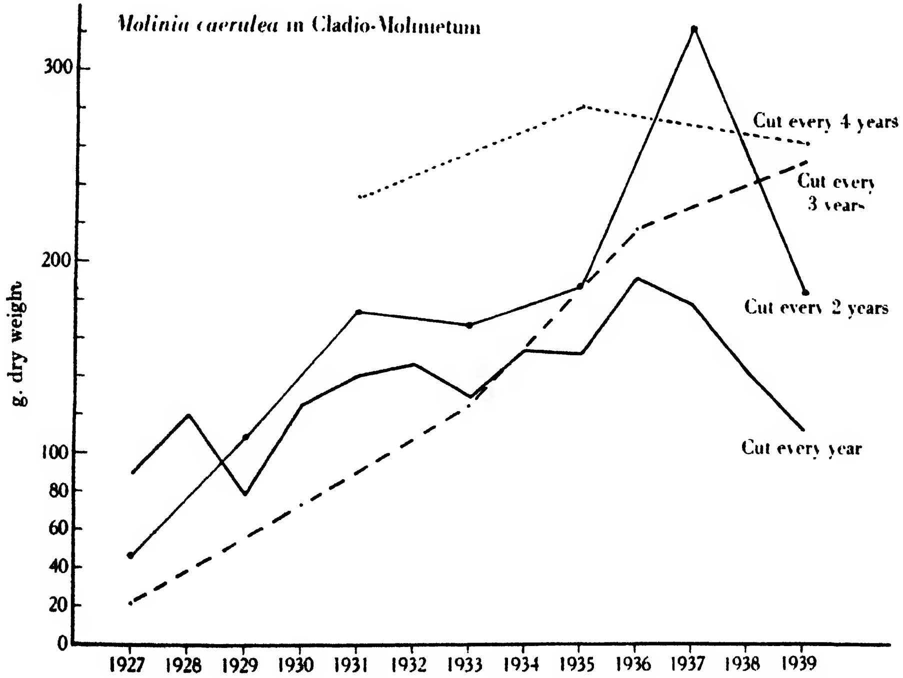

Fig. 14. Dry weights of *Molinia* produced in permanent metre-quadrats VI, VII, VIII and IX, in Cladio-Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. Under all frequencies of cutting the *Molinia* has increased.

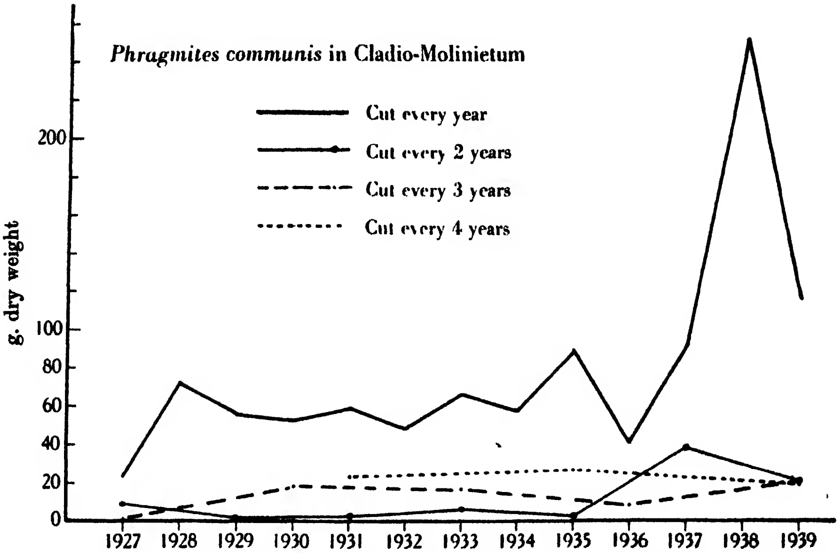

Fig. 15. Dry weights of *Phragmites* produced in permanent metre-quadrats VI, VII, VIII and IX, in Cladio-Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. The *Phragmites* crop seems to increase with more frequent cutting.

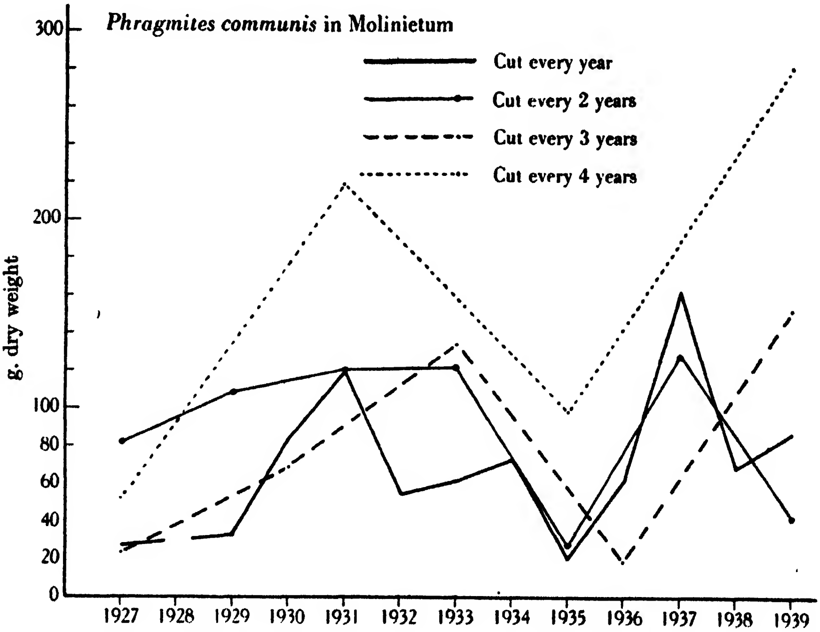

Fig. 16. Dry weights of *Phragmites* produced in permanent metre-quadrats I, II, III and IV, in Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. The crops are heavier than those in Cladio-Molinietum and show no clear response to varying frequency of cropping.

in Molinietum. The plant will evidently persist in considerable density under yearly cropping, and the data, though sparse, might indicate a tendency for the plant to increase under less frequent cutting. 1931, and perhaps 1933 and 1937, were favourable seasons, and 1935 less favourable.

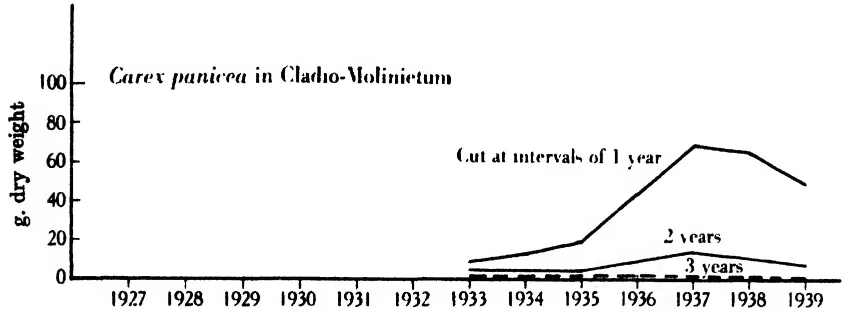

Fig. 17. Dry weights of *Carex panicea* produced in permanent metre-quadrats VI, VII, VIII and IX, in Cladio-Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. This species increases rapidly under yearly cutting, and much less rapidly with longer intervals.

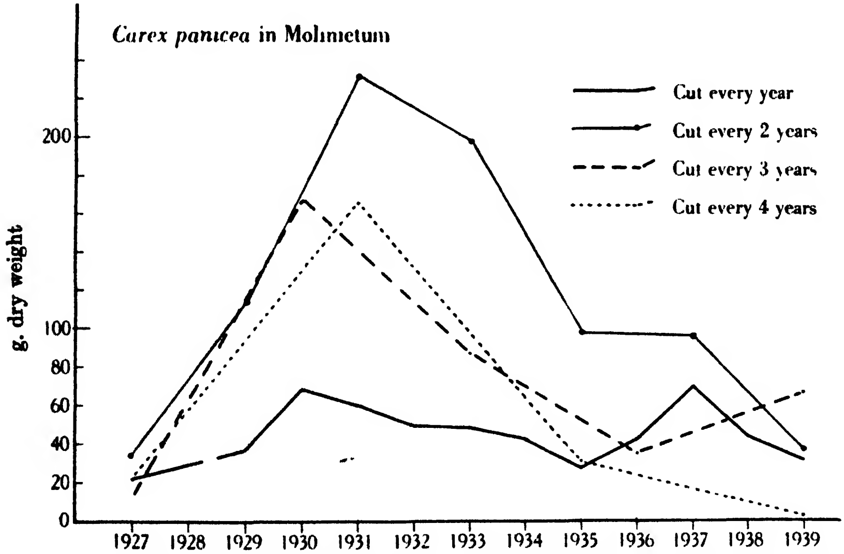

Fig. 18. Dry weights of *Carex panicea* produced in permanent metre-quadrats I, II, III and IV, in *Molinietum*, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927. There is a very large variation in yield from year to year.

A summary of the favourable and unfavourable seasons is given on p. 104. Although the pronounced irregularities in the curves must be largely due to climatic causes, they show no very simple relationship to one another except that 1931 and 1937 were years of high yield for most species, and 1935 one of

	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939
					Favourable (high yields)								
Cladium mariscus	.	.	.	.	.	.	+	.	.	.	?	.	.
Molinia caerulea	.	.	.	.	+	.	.	.	.	.	+	.	.
Phragmites communis	.	.	.	.	+	.	.	.	.	.	+	?	.
Carex panicea	.	.	.	+	+	.	.	.	.	.	+	.	.
Juncus obtusiflorus	.	.	.	.	+	.	?	.	.	.	?	.	.
Total dry weight	.	.	.	.	+	.	.	.	.	.	+	.	.
					Unfavourable (low yields)								
Cladium mariscus	.	.	.	.	.	.	.	.	+	.	.	.	.
Molinia caerulea	.	.	+	+	.	.	.	.	.	.	.	.	.
Phragmites communis	.	.	.	.	.	.	.	.	+	+	.	.	.
Carex panicea	.	.	.	.	.	.	.	.	+	.	.	.	+
Juncus obtusiflorus	.	.	.	.	.	.	.	.	+	.	.	.	.
Total dry weight	.	.	+	.	.	.	.	.	+	.	.	.	.

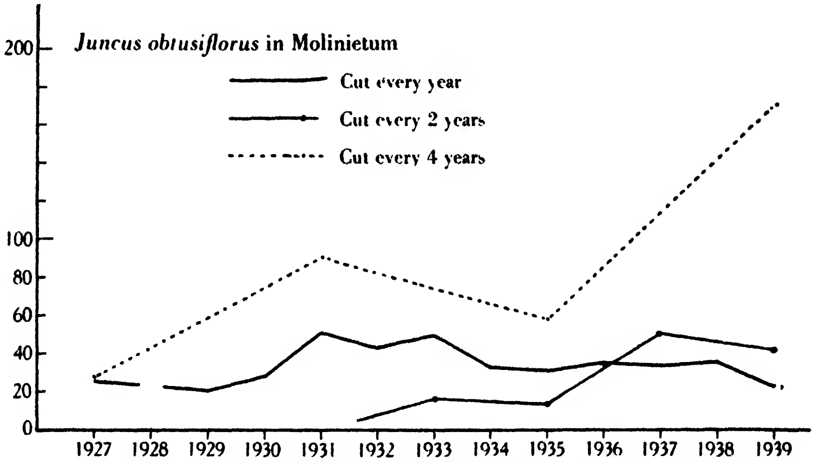

Fig. 19. Dry weights of *Juncus obtusiflorus* produced in permanent metre-quadrats I, II, III and IV, in Molinietum, cut at intervals of 1, 2, 3 and 4 years respectively, since 1927.

very low yield. Consideration of meteorological data yields no very evident explanation for this, but summer drought and late frosts in 1935 have already been mentioned as restricting the *Cladium* crop. Independent variations in the curves for individual species also show no simple relation to climatic features, and the data are unsuitable for close analysis.

SUMMARY

From abundant circumstantial evidence it had already been suggested that on Wicken Fen "litter" communities (Molinietum) had been produced by yearly autumn cutting of fen vegetation for cattle bedding, and that the other main crop on the fen (Cladio-Molinietum) was determined by the customary 3- or 4-yearly cutting. Field experiments carried on since 1927, and some observations since 1923, support this view strongly, and thus the author's view that these communities are stages in deflected successions. After

12 years of annual autumn cropping an area of Cladio-Molinietum had developed most of the features characteristic of Molinietum, and similar changes were demonstrated to take place more slowly with cropping at longer time intervals, whilst with 4-yearly cropping the Cladio-Molinietum seemed unaffected.

The results are based upon field-notes of areas each 20 m. square, with remapping and dry weight analyses of the sorted crop from permanent metre-quadrats. The different methods support and supplement one another strongly. The details of the change from Cladio-Molinietum towards Molinietum involved the diminution or disappearance of *Cladium* and associated "mixed-sedge" species such as *Eupatorium cannabinum*, *Lythrum Salicaria*, *Peucedanum palustre* and *Salix repens*, var. *fusca*, with the appearance and spread, or merely the extension of the species characteristic of "litter", such as *Molinia* itself, *Carex panicea*, *Juncus obtusiflorus*, *Scabiosa succisa*, *Valeriana dioica*, *Cirsium anglicum*, etc.

To some extent the reasons for these changes can be found in the plants themselves; thus the species typical of Cladio-Molinietum are tall, and those of Molinietum dwarfer. The latter therefore benefit by removal of competition of the taller species (the question of complementary requirements or interdependence probably does not affect most of the species). The *Cladium* is susceptible to frequent cutting because it has long-lived evergreen leaves, whilst *Molinia*, which is unaffected by autumn cutting, has annual shoots shed from the food-storing stem bases. *Carex panicea* appears particularly susceptible to competition.

A quadrat in vegetation brought by yearly cutting to a condition between Cladio-Molinietum and Molinietum, but left uncut since about 1918, has shown how changes towards a "litter" character are reversible when cutting is suspended. *Carex panicea* disappears again, *Molinia* is reduced and the dominance of *Cladium* is re-established.

Experimental areas in Molinietum cut at intervals of 1, 2, 3 and 4 years since 1927 have shown no very marked alteration in composition, although there has been some diminution of species characteristic of "litter" in the areas cut least frequently.

In both Cladio-Molinietum and Molinietum there are very large variations in the crop from one year to another, but although these are probably caused by seasonal differences in climate, it is difficult to connect them with any specific climatic indices.

Lastly we may note that the results call attention to the value of the method of dry weight analysis of the sorted crop from permanent metre-quadrats, in recording changes in the amounts of species of high frequency, such as the dominants and sub-dominants. This field descriptions fail almost entirely to do, and remapping of the quadrats does incompletely. The field descriptions, on the other hand, record changes in species of lowest frequency which are missed by the other two methods.

The author would, in conclusion, like to express his gratitude to Profs. S. M. Wadham and A. G. Tansley who encouraged the early undertaking of these experiments; Prof. Wadham himself made the first mapping of quadrat XII in 1923. Thanks are also gratefully given to my wife, who mapped other quadrats, and to the laboratory attendants and fen-keepers who helped in collecting crops and maintaining the cutting of the experimental areas.

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STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

VII. BRYOPHYTES AND LICHENS IN CHALK GRASSLAND, WITH A COMPARISON OF THEIR OCCURRENCE IN OTHER CALCAREOUS GRASSLANDS

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In the useful series of papers by Watson, published in this *Journal*, on the bryophytes and lichens of various British habitats, that dealing with calcareous soil (Watson, 1918) pointed out that a detailed account of the cryptogamic flora of the chalk could not be given, as it had been insufficiently investigated. Since then some details have been given of the cryptogamic flora of chalk beechwoods (Watson, 1936). The data in the present paper, which refers only to the natural grassland of the chalk, are partly derived from records made on the South Downs by Tansley & Adamson (1925, 1926) but mainly from observations by the writer during the last few years. Most of the information in the first section ("Ecological features") has already been published by Tansley (1939, pp. 540–1).

Ecological features

The commoner bryophytes may be placed in three groups, which are of course not sharply separated.

(*a*) The most constant species, in approximate order of importance, are:

Brachythecium purum
Hylocomium triquetrum
H. squarrosum
H. splendens
Dicranum scoparium
Camptothecium lutescens
Hypnum cuspidatum
Fissidens taxifolius

(*b*) Species which are probably present in many areas, but not often recorded and seldom playing a conspicuous part in the community:

Brachythecium rutabulum
Eurhynchium praelongum
Fissidens adiantoides
Hypnum chrysophyllum
H. cupressiforme (with var. *elatum* and intermediates)
H. molluscum
Mnium affine
M. undulatum
Thuidium abietinum
T. tamariscinum

(*c*) Species rarely met with, but generally playing an important part on the few areas where they occur (see p. 108):

Neckera crispa
Rhacomitrium lanuginosum
Frullania tamarisci

(*d*) A set of acrocarpous species of the genera *Weisia*, *Trichostomum* and occasionally *Barbula* which, frequently with *Fissidens taxifolius*, play an important part in some of the driest places where the turf is short or open. *Tortula ruralis* is sometimes abundant in places devastated by rabbits. .

Among the mosses in group (*a*), the only one of really high constancy is *Brachythecium purum*, a very common grassland species which is found as an understorey in the great majority of the chalk grasslands investigated. Next come the Hylocomia, woodland or grassland mosses, which appear especially on relatively damp chalk grassland, particularly on northern exposures protected against the direct rays of the sun, and which are there often very luxuriant; *Dicranum scoparium*, a very common moss, more generally found on rather acid soil; and *Camptothecium lutescens*, which among the really common mosses of the community is one of the few classed as calcicolous by Watson (1918).

Of the mosses in groups (*b*), (*c*) and (*d*), *Hypnum chrysophyllum*, *H. molluscum*, *Neckera crispa* and the *Weisia* and *Trichostomum* species are calcicole. In group (*b*) *Hypnum cupressiforme* is the most abundant moss, occurring in many sites with short grass, especially those which are rather dry. The *Mnium* species are restricted to the damper sites, such as northerly slopes, where they occur under thickly grown herbage. *Neckera crispa*, in group (*c*), is usually an inhabitant of bare limestone rock, and on the chalk is most commonly seen on the sides of cuttings too steep for a complete cover to be established. *Rhacomitrium lanuginosum* is a mountain moss, and has been recorded from one locality only, the relatively lofty region of War Down and Butser Hill in Hampshire, where the rainfall is high. Here it was locally abundant not only on flat partly leached ground, but also on a quite steep slope where the surface soil gave a distinct effervescence with acid. The liverwort *Frullania tamarisci* occasionally plays a conspicuous part on heavily grazed and unusually damp northern exposures with a large moss flora. Some species, for instance *Barbula cylindrica* and *Thuidium abietinum*, are much commoner in late stages of the sere leading from a bared surface to chalk grassland than they are in the mature community.

Lichens, although not uncommonly present, are rarely conspicuous in chalk grassland. In these cases the turf is always short and *Cladonia rangiformis* is the only important species. Only once or twice has it been seen as a very abundant constituent of the cover, the most notable instance being in the turf on the cliff-top at Cuckmere Haven in Sussex. According to Allorge (1922) *Cladonia rangiformis*, with *C. foliacea* var. *endiviaefolia* ("*Cladonia convoluta*", especially common in the Mediterranean region), is the most abundant lichen of rabbit-devastated chalk grassland in the Seine-et-Oise department in France. It is also reported by Litardière (1928) from chalk grassland in northern France.

Floristic data

The species recorded from chalk grassland are given in Table 1. The nomenclature for bryophytes follows the Census Catalogues of the British Bryological Society (1926, 1930), and for lichens Lorrain Smith (1918, 1926). The list is largely the result of a general ecological study of about fifty areas of chalk grassland on the South Downs, and not of a deliberate search for bryophytes and lichens, and could be enlarged, especially in regard to the smaller acrocarpous species, though only by additions which are ecologically quite unimportant (e.g. list below). It refers only to chalk grassland which is mature or in the late stages of its development by colonization of bared ground (Tansley & Adamson, 1925; Hope-Simpson, 1940). A study of chalk cuttings, of dense chalk scrub, of areas where the grass cover has been severely disrupted by rabbits and replaced by plants such as *Sedum acre*, or of other open chalk habitats, would probably reveal a good many additional species. A few species, found only on "chalk heaths" (whose surface soil, though forming only a thin layer over the chalk and derived from it, is acid all over), are omitted, but those occurring only on partially leached areas are included (*l* in column 1); for these no observations have been made as to whether or not the surface was acid on the spots where the species was growing. It is probable that some of them were in fact occupying restricted patches of acid soil, and that this was also the case with a few other species (e.g. *Polytrichum piliferum*) even where no evidence of local leaching was detected. The frequent occurrence of cases of a similar kind has been noted by Watson (1918).

The list in Table 1 does not exhaust the bryophyte and lichen flora of chalk grassland. Dr W. Watson has kindly informed the writer of the following additional species which he has observed in chalk grassland in Sussex and Surrey:

Bryum pendulum
Dicranum bonjeani
D. scoparium var. orthophyllum
Encalypta vulgaris
Eurhynchium crassinervium
Fissidens decipiens
Hypnum cupressiforme var. tectorum
Mnium rostratum
Phascum curvicolle
Lophocolea cuspidata

Cladonia foliacea
C. foliacea var. endiviaefolia

Even the list as it stands in Table 1, containing fifty-nine bryophytes and seven lichens, suggests a fairly plentiful cryptogamic flora, but it should be realized that many of the species have only been recorded once or twice. Furthermore it may be seen from column 1 that sixteen of the species have been found only in chalk grassland which is either immature or to some extent leached. Of the remainder, only about eight are commonly plentiful (see above, p. 107 (*a*)).

Table 1. *Bryophytes and lichens recorded from chalk grassland*

Column (1) gives particulars about the occurrence of the species in chalk grassland. *cg*, found in mature, entirely unleached grassland, but not necessarily limited to it; *s*, not recorded from such grassland but found in later stages of the sere leading to it after colonization of bared ground; *l*, not recorded from mature, entirely unleached grassland; occurring in association with calcifuge plants such as *Calluna vulgaris* and *Potentilla erecta* in grassland whose soil shows leached patches.

Column (2) indicates by *lg* the commoner species of Carboniferous Limestone grassland as recorded by Watson (1918 and *in litt.* All the other species in the table except *Polytrichum piliferum* and *Rhacomitrium lanuginosum* have, however, been observed by him in Carboniferous Limestone grassland).

Column (3) shows the relation to calcium carbonate according to Watson (1918). *cc*, calcicole; *ic*, indifferent but with slight preference for lime; *i*, indifferent; *cf*, calcifuge.

	(1)	(2)	(3)
Bryophytes:			
Anomodon viticulosus	s	lg	ic
Barbula cylindrica	cg	lg	cc
B. fallax	cg	lg	—
B. rigidula	s	—	cc
B. rubella	s	—	—
B. unguiculata	sl	—	—
Brachythecium glareosum	cg	lg	cc
B. purum	cg	—	—
B. rutabulum	cg	lg	i
B. velutinum	s	—	—
Bryum caespiticium	cg	lg	i
B. capillare	sl	lg	i
B. inclinatum	sl	—	ic
B. obconicum	cg	—	—
B. pallens	cg	lg	i
Camptothecium lutescens	cg	lg	cc
Ceratodon purpureus	cg	lg	—
Cylindrothecium concinnum	s	lg	cc
Dicranum scoparium	cg	lg	i
Ditrichum flexicaule	cg	lg	cc
Eurhynchium praelongum	cg	—	i
E. striatum	cg	—	i
E. swartzii	l	lg	ic
Fissidens adiantoides	cg	—	—
F. taxifolius	cg	lg	—
Hylocomium splendens	cg	lg	—
H. squarrosum	cg	lg	i
H. triquetrum	cg	—	i
Hypnum chrysophyllum	cg	lg	cc
H. cupressiforme + var. elatum	cg	lg	—
H. cupressiforme var. ericetorum	cg	lg	—
H. cuspidatum	cg	lg	i
H. molluscum	cg	lg	cc
Mnium affine	cg	—	—
M. stellare	cg	lg	—
M. undulatum	cg	—	i
Neckera complanata	cg	—	i
N. crispa	cg	lg	cc
Polytrichum piliferum[1]	cg	—	cf
Pottia lanceolata	l	—	—
P. minutula	s	—	—
Rhacomitrium lanuginosum	cg	—	cf
Seligeria calcarea	cg	—	cc
Thuidium abietinum	cg	—	—
T. tamariscinum	cg	—	i
Tortula ruralis	cg	—	ic
Trichostomum crispulum	cg	lg	cc
T. tortuosum	cg	—	cc

[1] Very exceptional; cf. text, p. 109.

Table 1 (*continued*)

	(1)	(2)	(3)
Webera carnea	s	—	—
Weisia crispa	cg	—	cc
W. crispata	cg	lg	cc
W. tortilis	cg	lg	cc
Frullania tamarisci	cg	—	—
Lophocolea bidentata	cg	lg	—
Lophozia turbinata	s	—	cc
Madotheca laevigata	cg	—	—
Pellia fabbroniana (=calycina)	s	—	—
Scapania aspera	cg	—	cc
S. nemorosa	cg	—	i
Lichens:			
Cladonia fimbriata	cg	—	—
C. furcata	cg	lg	i
C. pyxidata	cg	—	i
C. rangiformis (=pungens)	cg	lg	—
C. sylvatica	l	lg	—
Collema pulposum	cg	lg	—
Peltigera canina	cg	lg	i

COMPARISON WITH OTHER CALCAREOUS GRASSLAND

Carboniferous Limestone. Column 3 shows that twenty-eight of the bryophytes and five of the lichens are among the common ones in the grassland on Carboniferous Limestone, although all the others except the calcifuges *Polytrichum piliferum* and *Rhacomitrium lanuginosum* have been observed there by Watson. Of the bryophytes in the chalk grassland list which are not given as important constituents of Carboniferous Limestone grassland, two are important members of the chalk grassland vegetation. The striking case is that of *Brachythecium purum*, the most abundant bryophyte of chalk grassland and the only one of constancy 5, i.e. occurring in over 80% of the areas investigated (Tansley & Adamson, 1926). *Hylocomium triquetrum* is very abundantly found in chalk grassland and not reported among the common mosses of Carboniferous Limestone grassland.

On the other hand, sixteen bryophytes and about five lichens not appearing in the chalk grassland records upon which this paper is based are given as common in Carboniferous Limestone grassland:

Camptothecium sericeum[1]
Encalypta streptocarpa[1]
E. vulgaris[1], [3]
Eurhynchium pumilum
Fissidens decipiens[3]
Funaria calcarea[1]
Hypnum hispidulum var. sommerfeltii[1]
Mnium hornum
Plagiothecium denticulatum
P. undulatum
Thuidium philiberti[2], [4]

Tortula ambigua[1]
T. aloides[1]
Webera albicans[2]
Lophocolea cuspidata[3]
Plagiochila asplenioides

Peltigera polydactyla[5]
P. rufescens
Three or four Collemaceae, but these have not been carefully examined in chalk grassland

[1] Stony places.

[2] Damper sites.

[3] Found in chalk grassland by W. Watson (see p. 109).

The records of *Thuidium recognitum* for Carboniferous Limestone grassland probably refer to *T. philiberti* (Watson *in litt.*).

[5] Recorded from chalk heath (surface acid).

Our present knowledge of the environmental differences between the grassland of the chalk and that of Carboniferous Limestone does not make it possible to give definite reasons for these floristic differences. Some of them may be due in large measure to climate. The cryptogamic flora of the westerly chalk grasslands of Dorset and part of Wiltshire might approximate more closely to that of the Somerset limestone examined by Watson (1918) than does that of the South Downs, whence most of the present data are drawn, although the species important ecologically are the same in south-west Wiltshire as in Sussex.

Breckland. If we regard the grasslands of the Carboniferous Limestone as being, through their northerly and westerly location, more oceanic in character than chalk grassland, we can, on the other hand, recognize a drier, more continental type of calcareous grassland in the "grass-heath" of Breckland in East Anglia (Watt, 1940), although climate is not the only difference involved. One of the seven types of grass-heath recognized by Watt, that designated *B*, bears a stronger resemblance to chalk grassland than any of the other six types. The data are drawn from a very limited area and for this reason are not given in Table I where the juxtaposition of data from more extensive grasslands would give a misleading effect. It is, however, interesting to notice the resemblances and differences between the bryophyte and lichen elements of grass-heath *B* and of chalk grassland.

Of the forty-two species in Watt's list, the following twenty appear in the chalk grassland list of Table 1:

Brachythecium purum
Bryum capillare
Camptothecium lutescens
Ceratodon purpureus
Dicranum scoparium
Eurhynchium striatum
Fissidens taxifolius
Hylocomium splendens
H. squarrosum
H. triquetrum
Hypnum chrysophyllum
H. cupressiforme
Pottia lanceolata
Thuidium abietinum
Frullania tamarisci

Cladonia furcata
C. pyxidata
C. rangiformis
C. sylvatica
Peltigera canina

The relative abundance of these species, shared by grass-heath *B* and chalk grassland, differs in many cases. In particular, the most abundant members of grass-heath *B* are *Dicranum scoparium* and *Cladonia sylvatica*. On no areas of chalk grassland do these species play the leading part. Next comes *Hypnum cupressiforme*, which on the chalk is abundant only in rather dry, short turf.

It is not profitable to enumerate the chalk grassland species not recorded from grass-heath *B*. A fair comparison, i.e. one relating to the climatic and edaphic differences between the chalk and Breckland *B*, could only be made by considering a chalk area of similarly restricted extent under similar physiographic and biotic conditions. In respect of these conditions, as well as in area, chalk grassland as a whole covers a much wider range than the grass-heath *B* of Breckland. Nevertheless it is of interest to notice that two bryophytes which figure prominently in chalk grassland are absent from Watt's list for grass-heath *B*. These are *Hypnum cuspidatum* (usually an occupant of wet ground) and *Neckera crispa*. The former shows some preference for moister sites on the chalk, and the latter is particularly an occupant of steep slopes such as do not occur in Breckland.

On the other hand, the Breckland list contains twenty-two species which are not in the chalk grassland list of Table 1. They are:

Brachythecium albicans
Bryum roseum
Climacium dendroides
Encalypta vulgaris[1]
Eurhynchium megapolitanum
Hylocomium rugosum
Hypnum schreberi
Mnium rostratum[1]
Polytrichum juniperinum
Rhacomitrium canescens
Tortula ruraliformis
Weisia microstoma

Cephaloziella starkii
Lophocolea cuspidata[1]
Lophozia barbata
Ptilidium ciliare

Biatorina coeruleonigricans
Cetraria aculeata
Cladonia foliacea (= alcicornis)[1]
Diplochistes scruposus
Peltigera polydactyla
P. rufescens

In the very dry and chalky "grass-heath *A*" of Breckland, the most abundant member of the sparse bryophytic flora is *Ditrichum flexicaule*, which is rare in chalk grassland, while the two next most abundant, *Hypnum cupressiforme* and *Camptothecium lutescens*, are common on dry areas of chalk grassland. Among the rather numerous lichens of *A*, the principal one is *Cladonia rangiformis*, which is also the commonest on the grassland of the chalk. Only three of the other thirteen lichens of grass-heath *A* are recorded for chalk grassland.

The salient differences in occurrence and abundance of species emerging from the foregoing comparison of calcareous grassland types are summarized below. The headings are given in the shortest possible form. For example, "Carboniferous Limestone only" means that the species appear in Watson's records from Carboniferous Limestone, but that they are not among the chalk grassland species in Table 1 nor in Watt's list for Breckland *B*. The groups of species are arranged so that those specially characteristic of Carboniferous Limestone come first and of Breckland last, the chalk representing intermediate conditions. This arrangement particularly reflects decreasing moisture, which, whether of soil or atmosphere, is likely to be of paramount importance. Grazing conditions may also be an influential factor. Speaking very generally, grazing on Carboniferous Limestone grassland is due to sheep; on the chalk to sheep, cattle and rabbits; and on Breckland to rabbits only, in abundance.

(1) Carboniferous Limestone only. Seventeen of the twenty-one species

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[1] But observed in chalk grassland by Watson (see p. 109).

listed on p. 111 (the exceptions are *Encalypta vulgaris, Lophocolea cuspidata, Peltigera polydactyla* and *P. rufescens*, which do occur on Breckland *B*).

(2) Carboniferous Limestone and Chalk, not Breckland *B*. *Hypnum cuspidatum* (relatively hygrophilous), *Neckera crispa* (steep slopes and rock not found in Breckland).

(3) Chalk only. *Polytrichum piliferum* (exceptional occurrence), *Rhacomitrium lanuginosum* (local). Both are ordinarily calcifuge.

(4) More important on chalk than on Carboniferous Limestone, common on Breckland *B*. *Brachythecium purum, Hylocomium triquetrum.*

(5) More important on Breckland *B* than on chalk, occurring on Carboniferous Limestone but relative status doubtful. *Dicranum scoparium, Cladonia sylvatica.*

(6) Breckland *B* only. Eighteen of the twenty-two species listed on p. 113 (the exceptions are *Encalypta vulgaris, Lophocolea cuspidata* and the two *Peltigera* species, which are all common on Carboniferous Limestone).

(7) Commoner on Breckland *A* than on chalk, occurring on Carboniferous Limestone but relative status doubtful. *Ditrichum flexicaule, Hypnum cupressiforme, Camptothecium lutescens* (the two latter relatively xerophilous).

Attention should be drawn to two points in particular.

(1) The following figures are numbers of bryophyte and lichen species. (*a*) Total in the records considered for each grassland type. (*b*) Numbers "exclusive" to each grassland type, i.e. not in either of the other two types.

	(*a*)	(*b*)	
Carboniferous Limestone	54	17	
Chalk	66	2	See footnote below.
Breckland *B*	42	18	

The figures show that the chalk grassland list, although the longest of the three considered in this paper (but not necessarily with a richer flora per unit area), is almost wholly composed of species found on one or both of the other two grassland types; while each of these latter has a good many species peculiar to it.

(2) The species conspicuously commoner on the chalk than on Carboniferous Limestone (*Brachythecium purum* and *Hylocomium triquetrum*) are common on Breckland *B*; and those conspicuously commoner on the chalk than on Breckland *B*—in fact absent from the latter—(*Hypnum cuspidatum* and *Neckera crispa*) are also common on Carboniferous Limestone.

[1] An apparent discrepancy may be observed here in that the number of Carboniferous Limestone and Breckland *B* species which are not "exclusive", plus the two "exclusive" chalk species, amount to less than sixty-six. The explanation is that the figure of two is reached taking account of species observed on Carboniferous Limestone by Watson additional to those published (1918) which give the quoted figures of fifty-four and seventeen. These figures would both be larger if the species of Watson's unpublished observations were added, and the argument following would still be valid though based on different figures.

The facts given in the last two paragraphs indicate that the intermediate position occupied by chalk grassland in point of climatic, and to some extent biotic, factors is reflected in its bryophyte and lichen vegetation.

SUMMARY

1. Notes are given on the ecological roles of the principal bryophytes and lichens of chalk grassland.

2. The flora has not been exhaustively studied for its specific content, but a list is given of fifty-nine bryophytes and seven lichens which have been recorded.

3. This flora is compared with the list of species given by Watson as the principal ones in Carboniferous Limestone grassland. *Brachythecium purum* and *Hylocomium triquetrum* apparently play a more important part in grassland on the chalk than on Carboniferous Limestone.

4. Comparison of lists given by Watt (1940) for "grass-heath *B*" in Breckland shows considerable floristic similarity, but the Breckland list is richer in lichens and, considering the limited area, probably in bryophytes as well. The three principal roles in the two communities are played by different species. On the dry and chalky "grass-heath *A*" of Breckland, lichens are a more prominent feature than in any of the grasslands of the chalk.

5. The different conditions of moisture and grazing of the three types of calcareous grassland—Carboniferous Limestone, chalk and Breckland—are pointed out and the differences in their bryophyte and lichen vegetation summarized. The Carboniferous Limestone and Breckland *B* lists considered both contain a number of species peculiar to themselves (seventeen and eighteen respectively), while the chalk grassland list, though longer, contains only two species not found on one or both of the other two grassland types. The intermediate position of chalk grassland in regard to environmental factors is in fact reflected in the intermediate character of its bryophyte and lichen vegetation.

Dr W. Watson has kindly given much information and help in the preparation of this paper. He is, however, not committed to agreement with the statements made.

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PREHISTORIC CHARCOALS AS EVIDENCE OF FORMER VEGETATION, SOIL AND CLIMATE

By H. GODWIN and A. G. TANSLEY

In the last issue of this *Journal* (August 1940) Prof. Salisbury and Dr Jane published a study of charcoals[1] from three archaeological levels at Maiden Castle, Dorset, identified as Neolithic, Early Iron Age, and Late Iron Age respectively, and stated to be *ca.* 2500–2000 B.C., *ca.* 400–200 B.C., and *ca.* 50 B.C.–A.D. 50. These they compared with charcoals of the Roman period, obtained from excavations at Verulamium, and with charcoal made from hazel now growing on Dorsetshire chalk and Hertfordshire clay-with-flints. The extensive series of data presented are of great interest, but we feel that many of the inferences drawn should not pass without criticism.

(1) *Nature and origin of the woods represented.* "Most of the charcoal stems represented", say the authors, "are of comparatively small diameter and... were certainly in the nature of mere sticks or twigs." There was evidence that some at least of the wood was dead wood and there was "a very marked preponderance of certain species" (hazel and oak), but "a number of other species do occur". From these facts the authors infer (*a*) that the materials used were "collections of dead sticks either picked up or broken off", (*b*) that these were "collected locally and probably in the immediate vicinity of the site, as it is evident that the sticks from which the charcoals are derived were often too small to have been worth carrying a distance", (*c*) that the charcoals represent a random sampling of the woody vegetation growing where the wood was collected, and (*d*) that "since the great majority of the charcoals are either hazel or oak the community was probably a more or less closed one and not an open scrub" (p. 311). "In Neolithic times the chalk of Dorset was probably clothed with a closed plant community of woodland of the oak-hazel type" (p. 325).

Inference (*a*) seems to us plausible on the evidence, but the same cannot be said of (*b*), (*c*) and (*d*). Inference (*b*) is that the sticks identified "were often too small to have been worth carrying a distance". But when people living on an open down (which is the point questioned) needed firewood, would they not have been *obliged* to carry it from the nearest place where they could find it, even if that were at "a distance"? Can we not picture them dragging large branches over the ground, pushing them, butt foremost, into the fire, so that

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[1] E. J. Salisbury & F. W. Jane (1940). "Charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times", *J. Ecol.* **28**, 310–25.

the smaller half-burned twigs fell on its edge, or alternatively carrying armfuls of small dead sticks from the nearest wood to their village or camp and piling them on the fire, some falling on its edge and escaping complete combustion? The assumption that it is necessary to suppose the sticks were collected in the "immediate vicinity" seems to us quite gratuitous. The facts presented afford no basis for the conclusion that the downs themselves were "clothed, probably till late Iron Age times, with more or less closed woodland" (p. 312).

Inference (*c*), that the samples of charcoal identified represent "a rough approximation to the relative abundance of the different species", suggests several questions. Do all woody species burn equally well in open fires? Do some tend to become charcoal more readily than others? Can we assume that prehistoric man did not select or reject certain species for firewood as he certainly selected woods for other purposes? Does the dead wood of different species lying on a woodland floor represent, in approximately correct proportion, the woody species growing on the site, especially in view of the different tendencies of different species to shed twigs, or small branches, either spontaneously or under stress of competition for light, and in view also of differing rates of decay? All these possible sources of error in the inference are neglected by the authors.

Inference (*d*), that the downs were clothed with closed oak-hazelwood in Neolithic times, is vitiated by the insecurity of (*b*) and (*c*). We submit that no sound evidence is presented for any such belief.

(2) *Species represented in the charcoals of different ages.* Table 1 (p. 314) gives a summary of the woody species represented in the charcoals of the three periods, and of their frequencies of occurrence. It is unfortunate that the indications of presence or absence and of frequency are not clearly explained, and are very difficult to interpret with certainty. The different species, of which there are seventeen in all, are recorded in four different ways: as "present" with a percentage figure attached, as simply "present", by a varying number of crosses (×), and by a dash (—). Presumably a dash indicates absence, but it is not clear what the crosses represent. One might suppose that they must indicate presence and that their number (since this varies from six to ten) represents some rough approximation to the frequency of a given species at a given horizon. But on comparing the records in Table 1 with certain statements in the text it would seem that *crosses* mean absence.[1] If that is so why does their number vary and what do the dashes mean? It will thus be seen that it is impossible for the reader to make any sort of quantitative comparison between species that have no percentage figure

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[1] Thus buckthorn and whitebeam are stated in the text (p. 315) to be absent from the Early and Late Iron Age horizons, but they are recorded for these periods in the table by crosses, the former by nine and ten, the latter by seven and six respectively.

attached, or even to be sure whether those recorded by crosses are present or absent. Why did not the authors give the figures of the actual number of occurrences at the different levels? It may well be true that the Early Iron Age specimens were too few for statistical treatment, but in the absence of numerical statement the reader cannot, from the table, form *any* clear idea of the quantitative relations of the less frequent species.

The outstanding feature of this table is the great preponderance of hazel in the Neolithic (40%) and Late Iron Age (50%) charcoals, and of oak (Neolithic 23%, Late Iron Age 35%) in the same horizons. Both species are recorded simply as "present" in the Early Iron Age charcoal, of which comparatively few specimens were available. From the facts presented the authors conclude that "the general character of the flora is only consistent with a closed community such as might be represented by an oak-hazel coppice-with-standards at the present day, but with the difference that the hazel layer was not coppiced but probably grew as tall as in oak-hazel woods where the shrub layer is left uncut. In woods of this type the trees are normally infrequent...." We have seen how many possible objections to such a conclusion have been left unnoticed by the authors, and we cannot understand what they mean by the last sentence. *Natural* unexploited woods "of this type" are so rare in England to-day that no such statement can be legitimate. The paucity of trees in many oak-hazel woods may well be always due to their removal or to their failure to regenerate under existing artificial conditions. All that the evidence presented *proves* is that oak and hazel were species used as firewood by Neolithic and Iron Age man in Dorset. Possibly it also *suggests* the likelihood that they were available in greater quantity than other species within a practicable distance, a possibility no one would be disposed to deny.

Yew is recorded in the table as 8% of the wood in charcoal of the Neolithic level, "present" in the Early Iron Age, and recorded by seven crosses in the Late Iron Age. On p. 315 it is stated that yew "is absent from the Late Iron Age charcoals, and is represented by a single specimen only in the Early Iron Age charcoals, yet by no less than seven specimens in the Neolithic charcoals". If we regard yew as a calcicolous tree the statement is of course consistent with the authors' thesis that the soil of the site from which the charcoal wood was derived was progressively less calcareous in the three periods, provided we are willing to admit that the site where it actually grew was the same and that the number of specimens recorded is large enough to justify the inference. It was however unnecessary to base the claim of yew to be native in prehistoric times solely on Clement Reid's statement (1899) about its commonness in Neolithic peat of the Thames valley and the Fenland. Much more recently Erdtman (1928) showed that yew was very common in England in Sub-Boreal (Bronze Age) times, and Godwin & Clifford (1938) established the association of the tree in the Fenland both with Late Neolithic (in the modern and more exact definition of the term) and Bronze Age horizons. Still the occurrence of yew in the southern chalk region *ca.* 2500–2000 B.C. is a valuable new datum. Whether our authors' records establish its diminution in Dorset during the next 2000 years must remain highly dubious.

The absence of beech from all the charcoals examined leads our authors to say (p. 315) that "it would at least appear probable that this tree had not reached the Dorset chalk by the beginning of the first century A.D.". In this statement they lay far too much weight on *negative* evidence from a single site, and in adding that "even to-day there is some doubt as to whether the beech is native so far west" they overlook Hyde's records (Grimes & Hyde, 1935) of beech charcoal from an Iron Age site in south Wales, and of beech pollen in the early sub-Atlantic peat of a Glamorganshire bog (Fox & Hyde, 1939; Hyde, 1940), as well as the rather substantial amounts of beech pollen in Cardiganshire bogs down to the level of the *Grenzhorizont* (e.g. Godwin & Mitchell, 1938).

(3) *Supposed evidence for progressive leaching and subsequent erosion.* If we take buckthorn, whitebeam and yew[1] as probably inhabiting calcareous rather than non-calcareous soil, a diminution in frequency (or disappearance if crosses mean absence) of calcicolous woody plants is shown in passing from the charcoals of the Neolithic to those of the Iron Age. We have already suggested that the inference from frequency in charcoal to frequency of growing trees is a very dubious proceeding, particularly when it is based on so small a number of specimens, but, passing over this point, we find that the inferred diminution of the calcicolous element is attributed by Salisbury & Jane (p. 315) to "a steady augmentation of leached soil". "There is no reason to doubt that during the earlier part of the twenty to twenty-five centuries represented by our samples there would have been a steady augmentation of leached soil resulting in an ever-increasing thickness of clay, wherever the slope was not too great for its retention, the upper layers of which would become more and more depleted of their carbonates" (pp. 315–16).

If this progressive leaching is supposed to have been going on and to have been effective in so reducing the carbonate content of the soil as to alter the flora significantly during the last two millennia B.C., a period part of which at least is generally held to have been relatively dry, what, we may pertinently ask, was happening to the soil during the three preceding millennia, a period that has been generally held to have been relatively wet? Why was not the soil of the downs already poor in carbonates in Neolithic times? It is true that

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[1] It is perhaps doubtful if we should regard yew as an infallible indicator of calcareous soil. While it is perfectly true that the vast majority of English yews now grow on such soils, the tree is by no means confined to them.

the best opinion of archaeologists and pre-historians generally is beginning to question the validity, for these islands at least, of the clear-cut conception of a wet Atlantic and a dry Sub-Boreal period that has been generally accepted on the continent for many years. Evidence of a major climatic Atlantic—Sub-Boreal transition in Britain, comparable with the thoroughly well-established Boreal—Atlantic and Sub-Boreal—sub-Atlantic climatic changes, is often lacking, and there may perhaps have been several important alterations of climate between say 5500 and 500 B.C. But however this may be, it is certain that part at least of the Bronze Age in England was relatively dry, and there is not the slightest ground for supposing that soil which had remained unleached down to Neolithic times would be progressively leached through the Bronze Age.

So far as it goes the archaeological evidence still points to the southern chalk being drier in the Bronze Age, for in contrast to the Neolithic settlements on chalk summits (whether they were permanent "villages" or temporary "camps"), the chalk uplands seem to have been practically uninhabited during the Bronze Age, and this is at least plausibly attributed to deficiency of water. Barrows of Bronze Age type, on the other hand, are very numerous on the chalk downs, and the general view that the downs were grassland, used for traffic and grazing as well as burials, but not for settlement, is quite likely to be true and would correspond well enough with a climate inimical to the growth of trees. The Neolithic pits at Maiden Castle for instance were found to be "filled up and sealed by a thick and well-marked layer of turf before the Iron Age earthwork was built over and through them" (Wheeler, 1935, p. 267). At the base of this turf layer was a scatter of beaker sherds of early Bronze Age type, but the rest of the 1500 years or so which elapsed between the Neolithic and the advent of the Iron Age invaders is a blank so far as human settlement relics are concerned (Wheeler, 1937). A further and strong piece of evidence pointing to the conclusion that the downs were grassland in the Bronze Age is to be found in the "delicate outlines of the disc barrows" to which Mr O. G. S. Crawford (*in litt.*) has called our attention. He thinks (and we agree) that such structures cannot have been made in forest-covered land, nor could they have survived, in the beautifully preserved form they still show, a long period of colonization and occupation by woody plants. And it is quite inconceivable that they could have survived a long accumulation of leached soil.

Salisbury & Jane continue: "Hence it is not improbable that the floristic changes indicated by our material were a direct outcome of edaphic changes which would continue until the destruction of the forest covering, and with it the protective layer of humus, led to erosion and to gradual diminution of the clayey residue, or even complete exposure of the unleached chalky subsoil" (p. 316). Here they postulate a reversal of the process of clay accumulation, a reversal which they suppose to be consequent on increased destruction of forest during the Iron Age. Let us see what light the general body of geological and archaeological fact and inference that we now possess can throw on the history of soil and vegetation of the southern chalk during the periods with which Salisbury & Jane are dealing.

(4) *Surface geology and archaeological history of the chalk uplands.* The non-calcareous "clay-with-flints" as well as the extensive, relatively thin sheets of loam, not dignified by that name on the geological drift maps and often more or less calcareous, which now cover wide areas of chalk plateau and wide flat chalk summits, are generally held to have originated by continuous solution of the surface chalk through the action of percolating rainwater, leaving the scanty, insoluble fine mineral residue, mixed with flints where the original chalk contained flints, to accumulate slowly above the chalk subsoil. Besides the clay-with-flints and loams derived from the chalk itself there are widespread remnants of Tertiary deposits—often sandy—on the chalk plateaux. Thus most of the plateaux and many of the wider chalk summits are covered with (mainly) non-calcareous soil, and are to-day either cultivated or bear scrub or oakwood, and sometimes beechwood. Only on the escarpments, the sides of isolated chalk hills, and the steeper valley-sides is there any run-off of water which prevents the accumulation of leached soil, and it is on these and over the summits of the narrower ridges, where there is no considerable extent of flat ground, that we find the true shallow chalk soil (rendzina), the habitat of the chalk flora proper.[1]

The "erosion" of these steeper slopes is not a mechanical wearing away of the surface, but a continuous solution of the chalk by rainwater *beneath a covering of vegetation,* whether woodland, scrub or grassland, with a continuous removal of the insoluble residue down the slope. There are no "crags" or exposed rock surfaces on our southern chalk except the sea cliffs and the sides of old quarries, though steep slopes where rabbits have broken the vegetation cover are often covered with chalk rubble, and here mechanical erosion does occur locally. There can have been no general erosion of the plateaux themselves, whether they were or were not covered with trees and shrubs. The only places where the soil could become more calcareous is along the *edge* of a plateau abutting on a steep slope that is being worn back by solution, involving the edge of the leached plateau soil, which would then be very gradually washed down the slope. The bottoms of many dry chalk valleys are filled with non-calcareous rainwash from the slopes, but such deposits are nothing like voluminous enough to warrant a belief in large-scale erosion of leached

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[1] On parts of Salisbury Plain however there are considerable tracts of flat or gently sloping grassland which have a shallow unleached chalk soil. The causes of the difference between this soil and that of the typical down plateaux are not clear.

plateau soil. General erosion would no doubt occur under a climate of torrential rainfall, but there is no evidence whatever of such conditions during later post-glacial time. Thus the picture of a period of leaching and clay accumulation followed by one of general erosion, as presented by Salisbury and Jane, is entirely misleading.

In regard to the archaeological history of the chalk uplands we know that (apart from the Cotswolds and Mendips) Salisbury Plain, Cranborne Chase and the adjacent Dorset uplands were the areas of densest Neolithic settlement in southern England; and since the Neolithic people kept sheep and grew crops we must suppose that in the latter half of the third millennium many places in these regions were bare of trees. In the succeeding Bronze Age, as we have seen, there is little evidence of settlement, as opposed to burials, on the chalk uplands, but the evidence that they were generally grassland is strong (see p. 121). Wheeler (1937, p. 263) supposes "in the absence of detailed evidence" that "the bulk of the population" lived at this time in the valleys, a supposition quite consonant with dry conditions which made the downs themselves uninhabitable.

In the middle of the first millennium B.C. the climate became cool and wet: of the reality of that transition there is no doubt. This apparently coincided with the advent of invaders who used iron, and they resettled many of the Neolithic sites, suggesting that the chalk uplands now again became possible for human habitation. Tillage of these lands increased enormously during the later part of the Iron Age. "It is necessary to realise" wrote Crawford & Keiller (1928, p. 9) "that in Romano-British times practically the whole of Salisbury Plain, Cranborne Chase and the Dorset uplands were under the plough."[1]

Into some such general framework any interpretation of data from a particular locality must be fitted. Radical modification of the framework can only be admitted if new data from a considerable series of sites and definitely inconsistent with the general picture are brought to light. It need hardly be said that the data presented by Salisbury & Jane do not fulfil this requirement.

(5) *Width of tree-rings as evidence of climatic constancy or change.* Of all aspects of research into prehistory, none offers more difficulty than accurate estimation of past climates, and although we are unlikely, in this country, to be able to rival the remarkable performances of Huntington and Douglass in the analysis of tree-rings in relation to climate we probably have neglected much material of value for this purpose. Salisbury & Jane have now demonstrated that conversion into charcoal need not affect the value of tree-ring

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[1] It should be noted that these generalizations do not refer to the chalk plateaux covered with clay or loam, which now commonly bear woodland where they are not cultivated and which are very extensive to the north-east and east of the Dorset and Wiltshire areas.

measurements, and they give some evidence that in hazel grown on the chalk tree-ring width is directly related to rainfall. In hazel charcoal of Neolithic age they have measured 184 rings, of Early Iron Age 174, of Late Iron Age 578, and of recent growth 568. For these four groups they give the following mean widths (mm.): 1·16, 1·182, 1·185, 1·24, and remark "Although the differences between the mean values for the various periods are so small it is interesting to note that there is a very slight increase as we pass from the Neolithic charcoals to the Iron Age specimens and recent charcoals. This steady trend, if it have any significance would seem to suggest that there was a tendency for the climatic conditions to become steadily more humid from Neolithic times to the present day." But they immediately discount the suggestion by adding: "Actually, however, when we come to assess the differences between the means we find that in no instance is there a difference that is statistically significant" (p. 320), and conclude that "the data furnish no grounds for assuming any significant difference in the rate of growth of hazel during the past 4000 years" (p. 323). In their summary (p. 325) they assert that "from a statistical analysis objective evidence is furnished indicating that the climatic conditions throughout the period represented were probably essentially similar to those obtaining at the present time".

It must be pointed out that of the whole space of 4000 years or so between the Neolithic period and now our authors' data refer only to three periods, aggregating, at the outside, 800 years, and that the possibility of significant climatic changes in the intervals for which no data are available is ignored. Particularly the Bronze Age hiatus at Maiden Castle is passed over entirely without comment. It is true that their data "furnish no ground for assuming any significant difference in the rate of growth of hazel" *as between the periods represented by the horizons from which the samples were collected*, but equally they furnish very dubious grounds (as we shall see in a moment) for denying such difference, and no grounds whatever for denying the existence of climatic change in the much longer intervals separating these periods. Thus the assertion that there is "objective evidence" for essential similarity of climate "throughout the period represented" is quite without foundation.

The authors' method of handling the tree-ring data is open to serious criticism. In the first place it is not legitimate to use tree-ring data as a basis of comparison between trees grown on two different sites, unless these have similar conditions of soil, slope, exposure, spacing, etc. Far from giving positive evidence that the soil conditions were similar, our authors suggest that they had changed between the times when the different sets of specimens grew.

Further, we may note that though Salisbury & Jane rightly lay stress upon the importance of taking account of the progressive diminution of tree-ring width with the age of the tree, and give a diagram to illustrate it in hazel, they fail to recognize how much this factor actually impairs the data they present. The average width of rings of different years' growth in recent hazel wood appears from these data to be as follows:

Year	1st	2nd	3rd	4th	5th	6th	7th
Mm.	0·57	2·41	1·33	0·7	0·35	0·18	0·09

(6th and 7th extrapolated)

We presume that in any stem used for measurement of ring widths all the rings were measured, and we are told that "most were certainly of the nature of mere sticks or twigs". Since "specimens of charcoal of 2 or 3 years' growth have been omitted" we may consider for the purpose of illustration stems of 4 to 7 years of age. From the data given above for recent charcoal it would appear that in the same set of specimens the mean tree-ring width would be 1·37, 1·13, 0·82 or 0·72 mm., according to whether one measured the first 4, 5, 6, or 7 annual rings. The differences between these means are as large as those our authors obtained as a basis for determining the existence or non-existence of climatic change, and thus a difference in the mean age or in the distribution of different ages in the specimens measured from the four sets of charcoal might be responsible for most or all of the observed range of mean ring-widths, and equally might cancel differences really due to climatic change. The authors' statement that specimens of recent charcoal for comparison with prehistoric material have been obtained from stems of similar age does not adequately meet this criticism.

We suggest that comparison of tree-ring widths by determining the means of a large number of measurements of rings of different ages is valid only for the outer rings of large trees. For stems of the small age dealt with by the authors it would be proper to compare the widths of rings in equivalent numerical order from the centre of the stem—first rings with first, second with second, and so on. Taking the means of rings of all ages clearly introduces the disturbing element of the differences in width of rings of different ages which are dependent on the age factor itself.

Finally we would reiterate our sense of the value of such data as those collected by the authors. When similar data are available from many more sites they may well throw much light on past vegetational and climatic conditions. It would be most useful, also, if the authors would describe, for the benefit of other workers, their carefully worked-out methods of charcoal diagnosis and investigation.

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STUDIES ON THE VEGETATION OF MAURITIUS

III. THE STRUCTURE AND DEVELOPMENT OF THE UPLAND CLIMAX FOREST

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(*With Plates* 3 *and* 4 *and six Figures in the Text*)

The upland climax forest of Mauritius was briefly described in the first paper of this series (Vaughan & Wiehe, 1937) when it was pointed out that the present distribution of this community is restricted to small isolated blocks covering altogether an area of about 18 sq. km.

The site in which this investigation has been carried out was selected after a series of reconnaissance tours had been made in the upland forest. The object of these tours was to find a locality unaffected as far as possible by local variations in topography and soil, and where interference by exotic species and other secondary biotic factors had been as small as possible. It may be said that it is now impossible to find even a small area free from exotics, and there is no forest into which the ubiquitous *Ardisia crenata* (Arbre à Noel) and *Psidium Guyava* (Guava) have not penetrated. The preliminary work also included an examination of soils and listing species in quadrats of different sizes.

The area finally selected for study was the upland forest in Crownland Macabé, covering an area of about 800 ha. (*c.* 2000 acres) situated above the Black River gorges at an altitude of 550 m. Within this area ten sample plots, each 1000 sq. metres (50 m. by 20 m.), were taken at random, and all phanerophytes 10 cm. diameter at breast height and above were recorded, and classified according to their size classes. These results are shown in Tables 1 and 2.

It was important at this stage to ascertain whether the ten plots chosen were large enough in area and sufficiently uniform in composition to yield the necessary information required for a statistical analysis of the larger phanerophytes. This point is referred to later when the interpretation of the results is discussed.

For a more intensive and detailed study of the smaller woody species and young plants one of the 1000 sq. metre plots was chosen (sample plot no. 1). All phanerophytes in this plot 1 cm. diameter and above, or more than 50 cm. high, were measured, together with certain lianes, and their position mapped to a scale of 1–50 (Fig. 6).

The plot was prepared on the grid-iron method. A base line of 50 m. was laid down and longitudinal strips 2 m. wide and 20 m. long were charted.

This plot has now been suitably fenced off for protection against deer and pig, and all exotics uprooted. It is hoped to maintain this plot permanently, and although small, it will, with proper protection, serve for future investigations on the germination and distribution of native seedlings and other cognate problems.

The vegetation of the forest floor was examined by means of small quadrats varying from 1 to 4 sq. metres. One of these is reproduced in Fig. 4.

The development of the forest from the early stages of the sere was also investigated by means of 1000 sq. metre quadrats, so that the data obtained could be readily compared with that of sample plot no. 1. The communities selected were the *Philippia* heath occurring on unweathered lava, and the *Sideroxylon* thicket, a subclimax community of complex floristic composition. Comparative data were thus obtained illustrating the gradual changes taking place at different levels of the sere, and some knowledge was gained of problems connected with the development of the highly complex tropical woody vegetation.

In view of the importance of climatic factors in determining the distribution and density of epiphytes and lianes, a description of these synusiae has been postponed until sufficient data on the internal and external climate of the forest are available. Some of the woody lianes, the lower portions of whose stems are independent of support by woody plants, have been included in the chart of sample plot no. 1.

Observations on periodicity, biotic factors, and the autecology of certain species are still being collected and will form the subject of a separate publication. In the tables and lists of species, a query preceding a plant name indicates doubt as to its life form; a question mark after the generic or specific name indicates uncertainty with regard to identification. New or doubtful species bear on the herbarium sheet the ecological symbol which the plant was given in the field. A collection of the specimens, including new or undetermined species gathered during this investigation, has been deposited in the herbarium of the Mauritius Institute. For taxonomy and nomenclature, Baker's *Flora* (1877) has been used in conjunction with more recent papers on the vegetation of Mauritius. Full reference to these is given in Vaughan & Wiehe (1937).

Raunkier's scheme of life forms (1935) has proved most useful in the statistical work. His mesophanerophyte class has been divided into two subclasses, namely, α-mesophanerophytes 15 m. high and above, and β-mesophanerophytes 8–15 m. high.

The number of woody plants and lianes measured or recorded during this investigation was 10,375.

To avoid repetition and to facilitate reference, all plants mentioned in the text or figures have been arranged alphabetically in an appendix together with their vernacular name, family, distribution and life form.

CLIMATE AND SOILS

In 1938, a small meteorological station was established in this region, consisting of two Stevenson screens, one placed in the forest itself and the other in an open situation about a kilometre away; rain gauges have also been set up in the two localities. Data on rainfall, temperatures and humidity are being collected over a period of 18 months which, it is hoped, will yield useful information with regard to the internal climate of the community and its relation to "normal" conditions which prevail outside the forest. Meanwhile, some indication of the prevalent climate of the Macabé Plateau may be obtained from the data for Curepipe in Table 1 of the second paper of these studies (Vaughan & Wiehe, 1939) and in the comparative figures given at the end of this paper on p. 153. Briefly it may be said that the climate is characterized by a high rainfall of 3125 mm. per annum (about 125 in.), there being no distinct dry season, but a maximum precipitation coinciding with the hotter months from December to April. The mean annual temperature is about 20° C. (68° F.) with a daily range of about 6° C. (11° F.), the lowest mean minimum temperature, 14° C. (57° F.), usually occurring in July or August and the highest, 26° C. (79° F.), in January or February. Relative humidity is high throughout the year, fluctuating between 80 and 90, with an annual mean of 87.

As a consequence of the high rainfall prevalent in the uplands of the island, weathering of the parent rocks, mostly dolerites, has given rise to highly laterized acid soils of a peculiar yellowish colour which are rich in organic matter and poor in plant food elements. The physical properties of these soils vary according to the age of the parent rock. Mature soils derived from older rocks contain a smaller proportion of gravels and sand than the immature soils occurring on the Macabé Plateau which have been formed from more recent lava flows.

It is improbable that the difference between these two types of soils has played an important role in the development of the forest.

The figures reproduced below indicate the composition of the soils of the Macabé forest (12 in. samples).

Coarse sand %	Fine sand %	Silt %	Clay %	Organic matter %	Combined water %
43·7	6·1	20·2	21·0	9·0	16·66

Combined SiO_2 %	$Al_2O_3TiO_2$ %	Fe_2O_3 %	pH	P_2O_5 (Truogs)
0·2	33·8	39·3	5·4	0·0006

STRUCTURE

An inspection of the chart of sample plot no. 1 (Fig. 6) shows that the distribution of individuals is by no means random. Considerable patchiness is to be observed, and quadrats of less than 100 sq. metres give widely differing results. A scarcity of smaller woody species and young trees is usually evident in the neighbourhood of the largest trees, where the surrounding population is reduced as a result of root competition and the excessive shade of the canopy. In other places where a large top stratum tree has fallen or died, vigorous regeneration takes place resulting in the dense stocking and crowding together of second stratum species.

An examination of the figures in Table 1 indicates that when large plots of 1000 sq. metres are enumerated, the irregular distribution of individuals becomes smoothed out; in fact it may be said that plots of this size do give a very fair picture of the distribution and density of smaller woody species. The small number of individuals, 10 cm. diameter and above, in sample plot no. 1, is probably due to the presence in this plot of an unusually large number of top stratum species.

The results obtained from the measurements recorded on the ten sample plots, 1000 sq. metres in area, are presented in Tables 1 and 2. In Table 1 the number of individuals, 10 cm. diameter and over, occurring in each of the ten plots is shown together with the total for the whole area of one hectare. In Table 2 all the individuals in the ten plots are grouped together under their respective species into fourteen diameter classes.

An attempt may be made here to assess the whole phanerophytic population over an area of one hectare. The total number of individuals of 10 cm. diameter and over is given in Table 1. Smaller plants above 50 cm. high and 1 cm. diameter are charted in sample plot no. 1 (Table 5). Lastly, from a series of counts on the seedlings and young plants of the forest floor, an average value of the number of individuals per sq. metre is obtained. The mean total phanerophytic population per hectare may be summarized therefore as follows:

Trees, 10 cm. diameter and above	1,710
Shrubs, young or small trees less than 10 cm. diameter	16,000
Seedlings and young plants up to 50 cm. high ...	190,800
Total per hectare	208,510

Quantitative results which are available from other tropical forests indicate that the number of individuals of 10 cm. diameter and over in the Mauritius upland forest is remarkably high.

Some further points of interest with regard to the results expressed in Table 1 may be mentioned here. A preliminary examination of the whole area occupied by upland climax forest indicates that species of all life forms are fairly regular in their spacing. The majority of the species recorded in Table 1 seem to confirm this view which is exemplified by frequent species such as *Eugenia glomerata* and *Nuxia verticillata*, and the less common species of *Tambourissa* and *Diospyros*.

A notable exception to this uniform spacing is the gregarious species *Calophyllum Inophyllum* L. var. *Tacamaha* (Willd.) R.E.V. var. nov., which has a wide distribution with numerous varieties in the Mascarene Islands, Seychelles and the Indo-Malayan region. This species was formerly dominant over large though irregular tracts of the upland forest, where it displays a high germination capacity combined with exceptionally good regeneration. Its gregarious habit and wide distribution, characters so foreign to the Mascarene flora as a whole, are not without significance. There is reason to believe that it is a comparatively recent arrival, and that it has been able to compete successfully with, and in some cases supplant, the older well-established elements of the flora.

The seventeen hundred odd individuals recorded in Table 1 belong to fifty-two species giving a species individual ratio of 1 : 33. The individuals are distributed among the species in the following manner:

27	species with	1–20	individuals
12	,,	21–40	,,
3	,,	41–60	,,
2	,,	61–80	,,
4	,,	81–100	,,
4	,,	above 100	,,

The figures obtained in the size class classification (Table 2) may now be considered. The result of grading all the species in the ten sample plots into fourteen size classes makes it clear that the larger phanerophytes belong to two distinct life forms, and that the various species cannot be graded uniformly according to size in a continuous series. One group, the β-mesophanerophytes, comprising about thirty species, has an average diameter of 15–25 cm. at breast height; a second group includes about twelve species whose d.b.h. may reach a metre or more: these are the α-mesophanerophytes, the top canopy species of large trees.

The size class totals for the whole area have been expressed graphically in Fig. 1 A, where the fourteen size classes are plotted against the number of individuals of all species 10 cm. diameter and above. This curve is a frequency curve of a familiar form; it represents the summation of all the size class frequency curves of a number of phanerophytes belonging to different life forms. Its interpretation is therefore complicated by the variation in range in different species.

Table 1. *Individuals of* 10 *cm. diameter and over occurring in ten sample plots of* 1000 *sq. metres* (50 *m.* × 20 *m.*)

	Number of sample plot										
Species	1	2	3	4	5	6	7	8	9	10	Totals
Allophylus integrifolius Bl.	—	—	—	2	1	3	—	—	—	—	6
Antidesma madagascariense Lam.	1	—	—	—	1	—	1	2	1	1	7
Antirrhoea verticillata DC.	1	2	1	3	3	—	4	3	4	1	22
Aphloia theiformis Benn.	22	9	10	9	10	13	2	6	4	22	107
Apodytes mauritiana Planch	—	—	3	—	2	—	—	1	—	4	10
"Bois Caf-Caf" (Euphorbiaceae)	9	7	8	23	10	4	18	11	18	3	111
Calophyllum Inophyllum L. var. Tacamaha (Willd.) R.E.V.	—	—	—	—	4	1	2	9	—	—	16
Calophyllum parvifolium Bojer ex Baker	—	—	—	—	—	—	—	—	4	—	4
Calvaria major Gaertn.	2	4	4	2	4	4	1	2	3	7	33
Canarium mauritianum Bl.	2	2	—	—	2	1	5	2	1	1	16
Casaeria fasciculata Bojer ex Baker	—	—	—	7	7	8	6	—	4	9	41
Chasalia capitata DC.	1	—	1	—	—	—	—	—	—	—	2
Conopharyngia mauritiana (Poir.) R.E.V.	7	1	5	1	1	4	4	1	4	—	28
Diospyros sp. (Dx)	1	—	—	—	—	—	—	—	—	3	4
Diospyros spp. (D_9, D_{10})	1	4	4	4	4	6	4	5	4	2	38
Elaeodendron orientale Jacq.	7	8	3	19	7	11	9	10	5	17	96
Erythrospermum mauritianum Baker	10	—	7	—	—	2	6	5	2	5	37
Erythroxylon laurifolium Lam.	2	2	2	—	1	—	10	8	5	1	31
Eugenia cymosa Lam.	—	—	1	—	—	—	—	—	—	—	1
Eugenia glomerata Lam. (includes several sub-species)	21	40	26	28	20	36	24	47	18	40	300
Eugenia orbiculata Lam.	3	8	16	9	1	6	2	1	2	15	63
Eugenia sp. (Ej)	—	—	—	—	—	—	1	1	2	5	9
Eugenia sp. (E_{26})	—	—	—	1	—	—	—	—	—	—	1
Evodia sp. (E_{32})	1	—	—	—	—	1	—	—	—	—	2

Fernelia buxifolia Lam.	1	1	1	—	—	1	—	—	1	—	5
Gaertnera psychotrioides Baker	2	19	10	2	—	2	1	4	1	2	43
Geniostoma borbonicum Spreng.	—	—	—	2	—	1	2	2	—	1	8
Grangeria borbonica Lam.	—	—	—	—	1	—	1	—	—	—	2
Homalium paniculatum Benth.	—	—	—	1	—	1	2	8	1	2	15
Labourdonnaisia sp. (Lg)	7	—	14	—	—	—	—	—	—	2	23
Mallotus integrifolius Muell.-Arg.	2	1	—	1	10	8	14	11	15	20	82
Memecylon trinerva DC.	—	3	—	4	2	8	1	—	4	8	30
Mimusops maxima (Poir.) R.E.V.	1	8	3	10	15	3	32	9	15	13	109
Mimusops petiolaris Dubard ?	2	8	2	9	9	6	6	7	10	4	63
Molinaea arborea Gmel.	—	14	9	17	13	13	2	7	10	2	87
Molinaea cupanioides Radl.	1	—	—	—	—	—	—	—	—	—	1
Mussaenda Landia Poir. ?	1	—	—	—	—	—	—	—	—	—	1
Nuxia verticillata Lam.	11	6	9	8	11	14	11	11	7	8	96
Ocotea cupularis Cordem.	1	—	—	—	2	—	7	—	—	—	10
Olea lancea Lam.	—	1	1	—	1	—	7	1	4	—	15
Psiloxylon mauritianum Baill.	1	2	—	—	—	—	—	—	—	—	3
Quivisia oppositifolia Cav.	1	—	1	—	—	—	—	—	—	2	4
Rutidea coriacea Baker	—	—	—	1	—	—	—	—	1	2	4
Securinega durissima Gmel.	—	10	17	1	3	6	1	2	2	9	51
Sideroxylon Bojerianum A. DC.	—	1	—	—	—	—	—	—	4	—	5
Sideroxylon puberulum A. DC.	—	—	1	3	5	—	10	6	—	—	25
Tambourissa Sieberi DC.	3	—	3	4	1	3	2	—	2	3	21
Tambourissa spp. (T, Tp)	—	2	1	2	2	—	1	3	9	—	20
Trochetia triflora DC.	—	—	—	—	—	—	—	1	—	—	1
Xylopia Richardi Boiv.	1	—	—	—	—	—	—	—	—	—	1
Totals: Species 52, Individuals	126	163	163	173	153	166	199	186	167	214	1710

Table 2. *Size classes. Individuals of* 10 *cm. diameter and over occurring in one hectare of upland climax forest (summation of ten sample plots* 50 *m.* × 20 *m.)*

Size class, d.b.h. in cm. Species	10–14	15–19	20–24	25–29	30–34	35–39	40–44	45–49	50–59	60–69	70–79	80–89	90–99	100 and over	Totals
Allophylus integrifolius Bl.	2	3	—	1	—	—	—	—	—	—	—	—	—	—	6
Antidesma madagascariense Lam.	6	1	—	—	—	—	—	—	—	—	—	—	—	—	7
Antirrhoea verticillata DC.	14	7	1	—	—	—	—	—	—	—	—	—	—	—	22
Aphloia theiformis Benn.	71	25	9	—	2	—	—	—	—	—	—	—	—	—	107
Apodytes mauritiana Planch.	3	2	2	2	1	—	—	—	—	—	—	—	—	—	10
"Bois Caf-Caf"	90	18	3	—	—	—	—	—	—	—	—	—	—	—	111
Calophyllum Inophyllum L. var. Tacamaha (Willd.) R.E.V.	8	5	1	1	1	—	—	—	—	—	—	—	—	—	16
Calophyllum parvifolium Bojer ex Baker	—	3	—	1	—	—	—	—	—	—	—	—	—	—	4
Calvaria major Gaertn.	3	5	5	3	3	4	2	3	5	—	—	—	—	—	33
Canarium mauritianum Bl.	1	—	2	1	—	1	3	5	1	—	1	—	—	1	16
Casaeria fasciculata Bojer ex Baker	36	5	—	—	—	—	—	—	—	—	—	—	—	—	41
Chasalia capitata DC.	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Conopharyngia mauritiana (Poir.) R.E.V.	25	3	—	—	—	—	—	—	—	—	—	—	—	—	28
Diospyros sp. (Dx)	2	—	2	—	—	—	—	—	—	—	—	—	—	—	4
Diospyros spp. (D_9. D_{10})	27	7	2	—	—	2	—	—	—	—	—	—	—	—	38
Eloedendron orientale Jacq.	55	23	8	—	5	4	—	—	—	—	—	1	—	—	96
Erythrospermum mauritianum Baker	27	6	4	—	—	—	—	—	—	—	—	—	—	—	37
Erythroxylon laurifolium Lam.	30	1	—	—	—	—	—	—	—	—	—	—	—	—	31
Eugenia cymosa Lam.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Eugenia glomerata Lam. (includes several subspecies)	160	70	35	16	11	2	3	2	1	—	—	—	—	—	300
Eugenia orbiculata Lam.	48	11	4	—	—	—	—	—	—	—	—	—	—	—	63
Eugenia sp. (Ej)	8	1	—	—	—	—	—	—	—	—	—	—	—	—	9
Eugenia sp. (E_{26})	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1

Evodia sp. (E_{32})	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Fernelia buxifolia Lam.	3	2	—	—	—	—	—	—	—	—	—	—	—	—	5
Gaertnera psychotrioides Baker	39	4	—	—	—	—	—	—	—	—	—	—	—	—	43
Geniostoma borbonicum Spreng.	6	2	—	—	—	—	—	—	—	—	—	—	—	—	8
Grangeria borbonica Lam.	2	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Homalium paniculatum Benth.	5	4	2	3	1	—	—	—	—	—	—	—	—	—	15
Labourdonnaisia sp. (Lg)	11	5	2	1	1	—	—	1	2	—	—	—	—	—	23
Mallotus integrifolius Muell.-Arg.	66	13	2	1	—	—	—	—	—	—	—	—	—	—	82
Memecylon trinerva DC.	23	5	2	—	—	—	—	—	—	—	—	—	—	—	30
Mimusops maxima (Poir.) R.E.V.	31	19	8	6	12	16	7	5	1	2	—	1	—	1	109
Mimusops petiolaris Dubard?	17	15	11	6	4	3	2	1	2	2	—	—	—	—	63
Molinaea arborea Gmel.	46	25	13	3	—	—	—	—	—	—	—	—	—	—	87
Molinaea cupanioides Radl.	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Mussaenda Landia Poir.?	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
Nuxia verticillata Lam.	41	20	5	8	6	6	5	2	1	—	2	—	—	—	96
Ocotea cupularis Cordem.	7	3	—	—	—	—	—	—	—	—	—	—	—	—	10
Olea lancea Lam.	2	6	4	1	—	1	—	1	—	—	—	—	—	—	15
Psiloxylon mauritianum Baill.	2	—	—	—	1	—	—	—	—	—	—	—	—	—	3
Quivisia oppositifolia Cav.	3	1	—	—	—	—	—	—	—	—	—	—	—	—	4
Rutidea coriacea Baker	2	2	—	—	—	—	—	—	—	—	—	—	—	—	4
Securinega durissima Gmel.	31	8	7	1	2	2	—	—	—	—	—	—	—	—	51
Sideroxylon Bojerianum A. DC.	1	3	1	—	—	—	—	—	—	—	—	—	—	—	5
Sideroxylon puberulum A. DC.	15	3	2	—	3	—	—	—	—	1	1	—	—	—	25
Tambourissa Sieberi DC.	4	8	2	2	4	1	—	—	—	—	—	—	—	—	21
Tambourissa spp. (T, Tp)	11	5	3	1	—	—	—	—	—	—	—	—	—	—	20
Trochetia triflora DC.	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
Xylopia Richardi Boiv.	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Totals: Species 52, Individuals	990	349	144	59	57	42	23	20	13	5	4	2	—	2	1710

The size class frequency curves of some individual species are shown in Fig. 1 B. The large majority of species conform with the composite frequency curve, a good example being that of *Nuxia verticillata* (Fig. 1 B, circles). It is among the large top canopy species of α-mesophanerophytes that interesting abnormalities occur. The curve for *Mimusops maxima* rises to a maximum in the 35–40 cm. diameter class, and although this peak may not be significant, yet there are certainly fewer young and more middle-aged trees than in "normal" species.

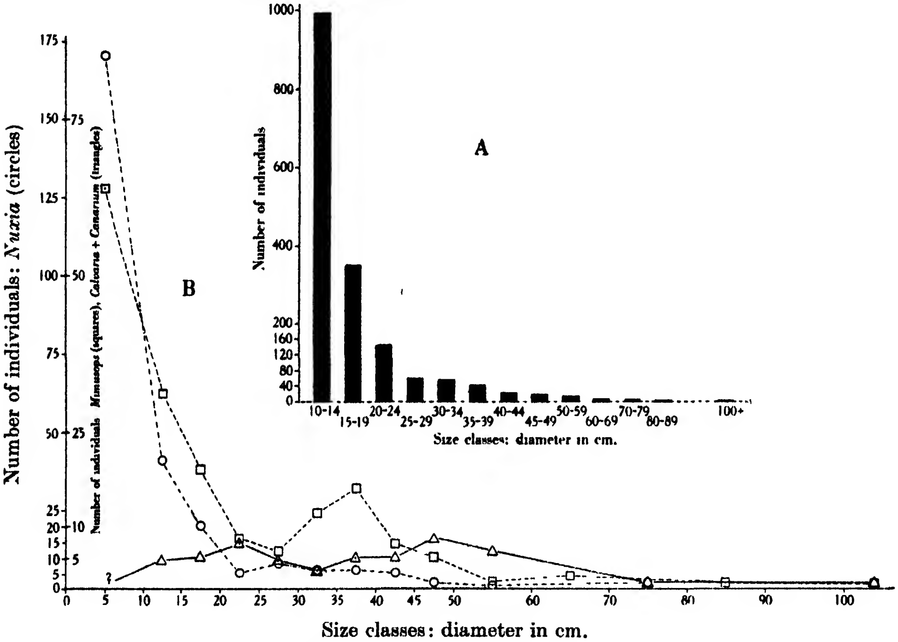


Fig. 1. Relation between size classes and number of individuals: A, for all species 10 cm. diameter and above in 1 hectare of upland climax forest, and B, for *Nuxia verticillata* (circles), *Mimusops maxima* (squares) and *Calvaria major* + *Canarium mauritianum* (triangles).

The growth data for *Canarium mauritianum* and *Calvaria major* resemble each other very closely, and have been united in a single curve (Fig. 1 B, triangles). Here also two peaks occur, but their significance cannot yet be confirmed; the curve, however, rises to a maximum in the 45–50 cm. size class, and no trees were found smaller than 10 cm. diameter. In the case of *Canarium* it is feared that natural regeneration must have ceased for a long period; no young trees of this species were found in the whole of the Macabé block, nor in fact in other localities where large trees are still living. The germination capacity of this species is about 20 %, and failure to regenerate is no doubt due to biotic factors, one notable example being the havoc played by monkeys in tearing down young flowering or fruiting branches.

Phot. 1. The buttressed trees are two immature individuals of the top canopy: *Eugenia glomerata* left and *Calvaria major* centre. A typical third stratum species with large leaves is seen in the top right hand corner. The flat-topped bush in the left foreground is *Psathura borbonica*, a co-dominant species of the fourth stratum. In the foreground is the looped stem of a rope climber (*Cnestis glabra*). The scale is a six-foot pole.

The germination capacity of *Calvaria* is of about the same order as *Canarium*, and should be sufficiently high to maintain the species under natural conditions. The germination and distribution of these remarkable woody seeds were probably assisted by their passage through the alimentary canal of the Dodo, and young seeds of this species have been unearthed with Dodo remains.

It may be noted that the flowering of these α-mesophanerophytes is often extremely irregular and by no means seasonal; even then flowering may take place without the setting of seeds.

The scantiness of young trees and their high survival value give these species of large trees an age-distribution curve resembling a human community in which birth control is rampant but death rarely occurs before sixty.

The introduction of deer, pig, and monkeys, and the rapid spread of certain exotic plants has undoubtedly had its effect on the regeneration of native species. However, the Mauritius forest flora is certainly a very ancient one, and long isolation, with its consequent freedom from competition with newer and more vigorous elements, may have enabled some of these large tree species to have survived in spite of a gradual diminution in their capacity for sexual reproduction.

STRATIFICATION

The existence of different size classes among the phanerophytes constituting the forest flora does not necessarily imply that the vegetation as a whole forms definite layers or strata, since the discontinuity might be obscured by young trees growing through the strata below on their way to join their own particular height class. As a result the forest might present a continuous vertical belt of vegetation from the ground flora to the topmost canopy trees. Now, in point of fact, the upland forest of Macabé does present to the observer a very marked stratification which is borne out by measurements obtained in sample plot no. 1, and clearly shown in the perspective drawing reproduced in Fig. 2. Important factors contributing towards this result are the relative proportion of young and mature individuals in each stratum, the difference in growth rates of individuals of varying heights and ages, and the characteristic physiognomy possessed by many species in particular size classes.

The stratification tables (Tables 3 A and B) have been compiled from data obtained during the mapping of sample plot no. 1 (Fig. 6), and comprise measurements of 1726 individuals distributed among 65 species. It is found that all the phanerophytes fall naturally into four groups: α-mesophanerophytes above 15 m., β-mesophanerophytes 8–15 m., microphanerophytes 2–8 m., and nanophanerophytes 0·5–2 m. high. A cross in a column indicates that there is evidence that the species belongs to the particular size class to which it is assigned, but that only young individuals were found in the plot. The characteristic features of the different strata may now be discussed.

Table 3 A. *Stratification of species: sample plot no.* 1 (*Fig.* 6)

	Strata				
Species	I Above 15 m.	II 8–15 m.	III 2–8 m.	IV 0·5–2 m.	Totals
I. α-Mesophanerophytes:					
Calvaria major Gaertn.	1	1	—	—	
Canarium mauritianum Bl.	4	1	—	—	
Elaeodendron orientale Jacq.	1	6	9	—	
Eugenia glomerata Lam.	5	31	126	25	
Ficus sp.	1	—	1	—	
Labourdonnaisia sp. (Lg)	2	7	10	1	
Mimusops maxima (Poir.) R.E.V.	1	—	—	1	
Mimusops petiolaris Dubard?	1	1	1	—	
Nuxia verticillata Lam.	2	15	14	4	
Tambourissa Sieberi DC.	2	2	8	1	
Totals	20	64	169	32	285
II. β-Mesophanerophytes:					
Allophylus integrifolius Bl.	—	×	3	1	
Antidesma longifolium Bojer ex Baker	—	×	1	—	
Antidesma madagascariense Lam.	—	1	—	—	
Antirrhoea verticillata DC.	—	1	—	—	
Aphloia theiformis Benn.	—	48	96	10	
"Bois Caf-Caf" (Euphorbiaceae)	—	28	25	1	
Conopharyngia mauritiana (Poir.) R.E.V.	—	30	98	8	
Diospyros sp. (Dx)		1	—	—	
Diospyros sp. (D_9)	—	1	—	—	
Erythrospermum amplifolium Thouars	—	3	6	—	
Erythrospermum mauritianum Baker	—	42	102	3	
Erythroxylon laurifolium Lam.	—	10	62	13	
Eugenia cymosa Lam.	—	2	12	—	
Eugenia orbiculata Lam.	—	9	54	8	
Eugenia venosa Lam.		5	43	2	
Eugenia sp. (Ej)	—	1	—	—	
Fernelia buxifolia Lam.	—	2	2	—	
Gaertnera psychotrioides Baker	—	5	10	—	
Gaertnera sp.?	—	—	—	1	
Geniostoma borbonicum Spreng.	—	1	—	—	
Ludia sessiliflora Lam.	—	1	1	—	
Mallotus integrifolius Muell.-Arg.	—	3	—	—	
Memecylon trinerve DC.	—	×	2	1	
Molinaea arborea Gmel.		×	10	9	
Molinaea cupanioides Radl.	—	1	—	—	
Mussaenda Landia Poir.?	—	1	—	—	
Ochna mauritiana Lam.	—	—	1	—	
Ocotea cupularis Cordem.	—	1	—	—	
Psiloxylon mauritianum Baill.	—	1	2	—	
Quivisia oppositifolia Cav.	—	2	—	—	
Securinega durissima Gmel.		1	—	—	
Tambourissa elliptica (Tul.) DC.?	—	×	4	—	
Tambourissa pedicellata Baker	—	×	25	3	
Xylopia Richardi Boiv.	—	2	—	1	
Totals	—	203	559	61	823
III. Microphanerophytes:					
Bertiera Zaluzania Comm. ex Gaertn.	—	—	3	—	
Chasalia capitata DC.	—	—	257	29	
Chasalia grandifolia DC.? (Cw)	—	—	6	2	
? Claoxylon linostachys Baill.	—	—	1	—	
Coffea macrocarpa A. Rich.	—	—	3	5	
Colea mauritiana Bojer	—	—	×	1	
Evodia sp. (E_{32})	—	—	×	1	
Leea sambucina Willd.	—	—	×	1	
Memecylon angulatum Reich.	—	—	10	16	

Table 3A (*continued*)

	Strata				
	I	II	III	IV	
Species	Above 15 m.	8–15 m.	2–8 m.	0·5–2 m.	Totals
III. Microphanerophytes (*continued*)					
? Memecylon cordatum Desv.	—	—	1	—	
? Molinaea macrantha Radl.			1	—	
Ochrosia parviflora G. Don	—	—	2	—	
Oncostemon latifolium Mez.	—	—	1		
Phyllanthus phillyreifolius Poir.	—	—	1		
? Pleurostylia sp. (p)	—	—	1	-	
Psathura terniflora A. Rich.? (P_{21})	—	—	9	—	
? Tambourissa amplifolia DC.	—		1	—	
Totals	—	—	297	55	352
IV. Nanophanerophytes:					
Acalypha colorata Spreng.	—	—	—	1	
Ixora sp. (Is)				32	
Psathura borbonica Gmel.	—	—	—	128	
Psathura myrtifolia A. Rich.	—	—	—	105	
Total	—	—	—	266	266
				Total	1726
No. of individuals in strata	20	267	1025	414	1726
No. of species in strata	10	33	41	23	—
Total no. of individuals of each life form	285	823	352	266	1726
Total no. of species of each life form	10	34	17	4	—

Table 3B. *Distribution of individuals of each life form in the four strata*

Life form	Mesophanerophytes		Mesophanerophytes		Microphanerophytes		Nanophanerophytes	
Strata	No. of individuals	%	No. of individuals	%	No. of individuals	%	No. of individuals	%
Above 15 m. I	20	100	—	—	-	—	—	—
8–15 m. II	64	24	203	76	—	—	—	—
2–8 m. III	169	16	559	55	297	29	—	—
0·5–2 m. IV	32	8	61	15	55	13	266	64

(i) *α-Mesophanerophyte stratum.* This life form includes twelve species, ten of which are recorded in sample plot no. 1. The top stratum formed by these species is very conspicuous, forming an open canopy of umbrella-shaped crowns with white lichen-covered branches towering above the dense assemblage of smaller phanerophytes beneath. As a rule the main bole is rather short and straight without lateral branches until it has emerged from the closed second stratum, above which it divides more or less equally into three or four stout spreading branches themselves dichotomously forked, with the leaves confined to dense whorls at the end of the ultimate branches.

The crowns of the big trees are seldom in lateral contact except where, owing to their very uneven distribution, four or five occur together in a somewhat restricted area. Seven of the twelve species belong to the family Sapotaceae and it is the individuals of this family, considerably outnumbering the remainder, which contribute mainly to the characteristic physiognomy of this stratum. Other families represented are: Moraceae (*Ficus*), Loganiaceae (*Nuxia*), Monimiaceae (*Tambourissa*), Burseraceae (*Canarium*) and Celastraceae (*Elaeodendron*). Eight species have leaves which are all more or less alike in shape and size and belong to Raunkier's "Mesophyll" size class; the remainder have "Microphyll" leaves. Common features of their anatomy are the thick epidermal tissues and waxy cuticle which serve the triple function of

Fig. 2. Perspective drawing of a section of the forest 20 m. × 2 m. as viewed by an observer standing at 15 ft. above ground level. The trees are drawn to scale and are shown in plan in Fig. 6 at 42–44 m. The large tree is *Mimusops maxima* the surface root system of which is shown in Fig. 3.

Phot. 2. The large tree on the right is *Canarium mauritianum*. There are no buttresses, but massive surface roots arise from the base of the trunk. On the left, with hollow bole, is *Tambourissa Sieberi*. The dominant species of the ground flora, *Pilea urticifolia*, is seen in the foreground.

protection from wetting, excessive insolation, and damage by wind. Flowers are small and inconspicuous though often numerous; cauliflory occurs in *Tambourissa.*

Buttressing is common in Sapotaceae and also in *Eugenia*; in Pl. 3, phot. 1, two young individuals of *Eugenia* and *Calvaria* are seen with well-developed buttresses. *Canarium* (Pl. 4, phot. 2) does not form buttresses, but massive surface roots often 30–40 cm. diameter are common.

The surface roots formed by so many species in the upland forest are a most striking feature of the forest floor. Fig. 3 represents a scale plan of the surface root system of *Mimusops maxima*; here the root system extends over an area of 300 sq. metres, and certain individual roots can be traced and their diameter measured for a distance of 17 m. from the end of the buttresses. The dotted line in Fig. 3 indicates the approximate spread of the crown, and it will be noted that the general form of the tree with its spreading flat-topped crown, short stout bole and immense lateral root system is well adapted to withstand the onslaught of violent cyclonic winds which sometimes attain a velocity of over 160 km. an hour.

The number of trees per hectare with a diameter of 50 cm. or more is twenty-five, and really large individuals, 1 m. diameter or more, rarely exceed 2–4 per hectare.

(ii) *β-Mesophanerophyte stratum.* The second stratum of small trees is of note on account of the great density of species, comprising as it does some forty species distributed among eighteen families. In this stratum no generalizations are really possible, the greatest variety being displayed in arrangement, form, and structure of leaves and flowers. Lateral branching usually begins at about 3–5 m. above the ground; the crowns are more or less oblong or pyramidal, and lateral branches of adjacent individuals overlap and interpenetrate so as to form a dense zone of vegetation rising to a height of 11–15 m. Rope lianes climb up and then spread over the top of the closed canopy, binding together the crowns of the small trees, and their stems continuing to grow become suspended in loops and coils (Pl. 3, phot. 1). The foliage of these climbers adds considerably to the leaf density of this stratum. A little under one-quarter of the individuals making up this stratum are young trees passing through on their way to the top canopy (Table 3B).

The families Myrtaceae, Flacourtiaceae, and Euphorbiaceae are well represented, but no particular species or family dominates this stratum in the same way that Sapotaceae do in the top canopy. Two deciduous species are occasional, *Ochna mauritiana* and *Tambourissa pedicillata*, though others are intermittently deciduous for varying periods, often regardless of season.

(iii) *Microphanerophyte stratum.* Under the dense shade cast by the closed second stratum of small trees, an open stratum of under-trees and shrubs occurs.

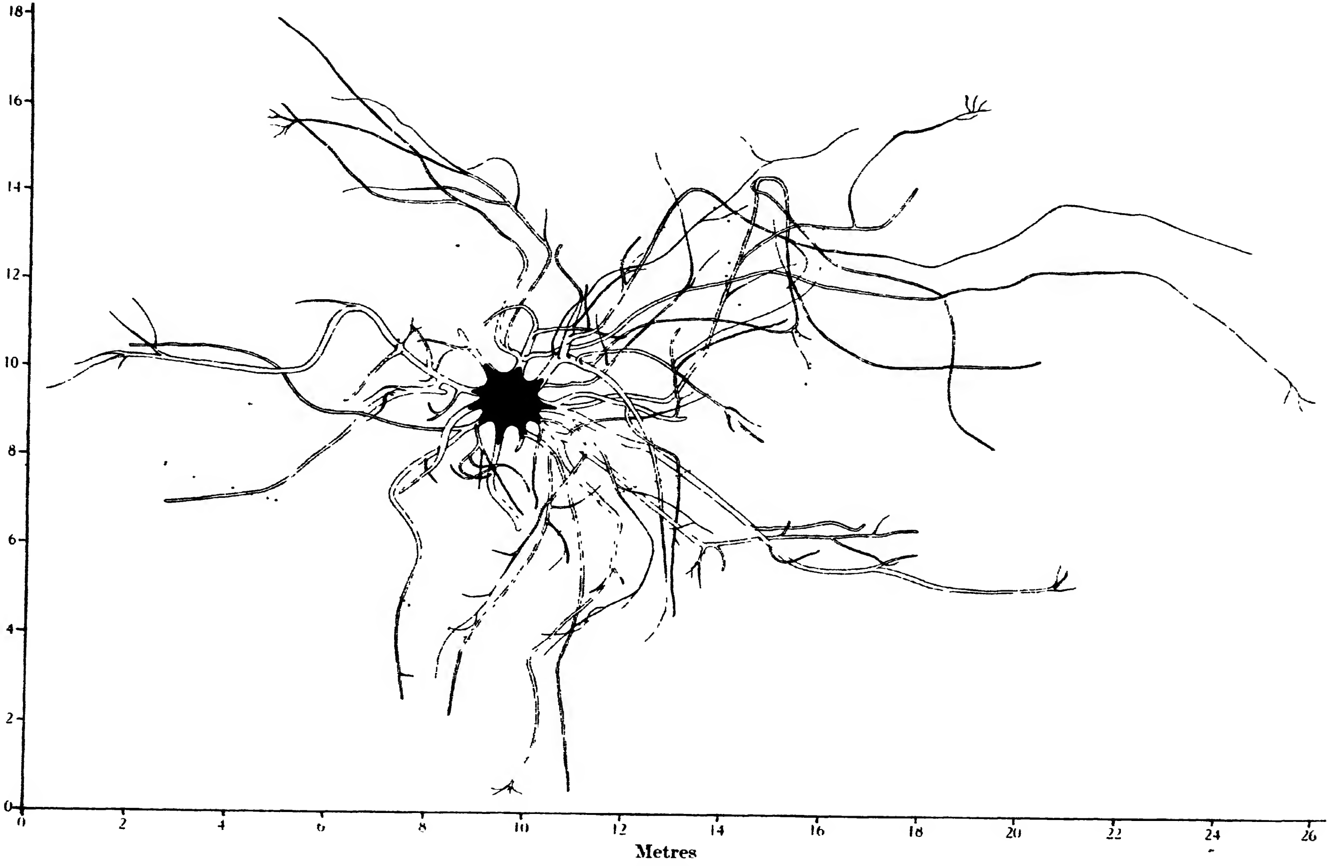


Fig. 3. Scale drawing of a typical surface root system. The portion blacked in represents cross-section of trunk and buttresses. The roots shown are those whose diameter could be measured without disturbing the soil. The approximate spread of the crown is indicated by the dotted line. This species is *Mimusops maxima* and is shown in Fig. 6 at 43 m. and 8 m.

There is no abrupt discontinuity between this stratum and the one above, but it is clearly a distinct zone, the population of which displays certain definite features. Many of these plants are characterized by their large leathery leaves borne at the end of a long, little-branched, slender stem; a good example is seen in Pl. 3, phot. 1.

Although flowers in this zone are usually small and inconspicuous, they show great diversity in number and arrangement; many are scented or rather odorous, and it is clear that the large majority are insect pollinated. The family Rubiaceae is dominant and nearly 90% of the individuals of this stratum, other than young trees belonging to higher strata, belong to the species *Chasalia capitata* whose slender branches spread themselves out fan-wise underneath the dense zone of vegetation above. Over 70% of the individuals in this stratum are young trees belonging to the α-meso- or β-mesophanerophyte strata.

(iv) *Nanophanerophyte stratum*. The society formed by small shrubs belonging to two species of the Mascarene genus *Psathura* (Rubiaceae) is one of the most distinctive features of the upland forest. They form low flat-topped, much-branched bushes usually about 3 to 4 ft. high (Pl. 3, phot. 1). Their density is about two hundred and fifty individuals in 1000 sq. metres. Other species occur occasionally, but their contribution to the physiognomy and general character of this stratum is not important.

The micro- and nanophanerophyte population may be regarded as somewhat scanty, and movement through the forest is little impeded by it. A moving figure fades from view at about 50 m., but this is due chiefly to the closely packed boles of top and second strata species.

Fig. 2 is a scale elevation or profile of a section of the high forest, and is an attempt to show the habit of some of the species and to give a general view of stratification. The crown of the large tree, *Mimusops maxima*, which has not yet reached its full height, is seen emerging from the closed second stratum; the bottom stratum of nanophanerophytes may be readily distinguished.

To conclude this section on stratification a family dominance table is given below for all phanerophytes recorded in sample plot no. 1.

(v) *The ground flora*. The ground flora may conveniently be considered as comprising (*a*) the ground flora proper consisting in the main of low herbaceous plants, (*b*) seedlings of the phanerophyte population, (*c*) cryptogamic flora.

It has already been pointed out that the woody elements of the forest flora show considerable variation in leaf form and other characters, a feature which seems to become more pronounced as the lower zones or strata of the forest are reached. It is perhaps due to the remarkable uniformity of climatic conditions which obtain within the forest that so much diversity is possible. This is evident also in the ground flora, although nearly all the species are confined to the two families Urticaceae and Orchidaceae. Two small-leaved species of *Pilea*, *P. atroviridis*, and *P. urticifolia*, are dominant (Pl. 4, phot. 2). Within the same genus another species with leaves 5–7 cm. long is occasional, and a third species, *P. verbascifolia*, a robust plant with leaves up to 20 cm. long, is quite common. The terrestrial orchids also exhibit great variety. Some are solitary with small thin silvery or purple leaves often with a few very minute flowers; these forms are well exemplified by *Gymnochilus nudum*, *Dispersis oppositifolia*, *D. tripetaloides*, *Benthamia* sp. Contrasting markedly with these are robust tall-growing gregarious species including *Calanthe sylvatica* and three species of *Phajus*, *P. tetragonus*, *P. villosus*, and *Phajus* sp., all of which have large prominently veined leaves and showy or conspicuous flowers.

Table 4. *Family dominance. Relation between family/species and family/individuals for all phanerophytes recorded in sample plot no.* 1 (*Fig.* 6), *upland climax forest*

Family	Species	%	Individuals	%
Rubiaceae	13	19·7	601	34·86
Euphorbiaceae	8	12·1	63	3·65
Myrtaceae	5	7·7	323	18·73
Flacourtiaceae	4	6·1	312	18·10
Monimiaceae	4	6·1	46	2·67
Sapotaceae	4	6·1	27	1·57
Sapindaceae	4	6·1	25	1·44
Melastomataceae	3	4·5	30	1·74
Apocynaceae	2	3·0	138	8·00
Loganiaceae	2	3·0	36	2·09
Celastraceae	2	3·0	17	0·99
Ebenaceae	2	3·0	2	0·12
Linaceae	1	1·5	85	4·93
Burseraceae	1	1·5	5	0·29
Annonaceae	1	1·5	3	0·17
Lythraceae	1	1·5	3	0·17
Meliaceae	1	1·5	2	0·12
Moraceae	1	1·5	2	0·12
Bignoniaceae	1	1·5	1	0·06
Lauraceae	1	1·5	1	0·06
Myrsinaceae	1	1·5	1	0·06
Ochnaceae	1	1·5	1	0·06
Rutaceae	1	1·5	1	0·06
Vitaceae	1	1·5	1	0·06
Totals:	65	—	1726	—
Families 24				

The seedling and young plant population includes all individuals not exceeding 50 cm. high. Counts were made in fifty 1 sq. metre quadrats thrown at random and a mean value of 19·08 individuals was obtained. The previously recorded figure of thirty individuals (Vaughan & Wiehe, 1937, p. 311) must be regarded as too high. Unfortunately a large number of the young seedlings have not yet been identified; in consequence little is known about their distribution and relative frequency. A typical quadrat of the forest floor is reproduced in Fig. 4. Ferns, mosses and hepatics are rare on the forest floor; plants which appear to be growing on the ground are nearly always found on closer examination to be attached to rotting wood or the partly exposed roots of trees.

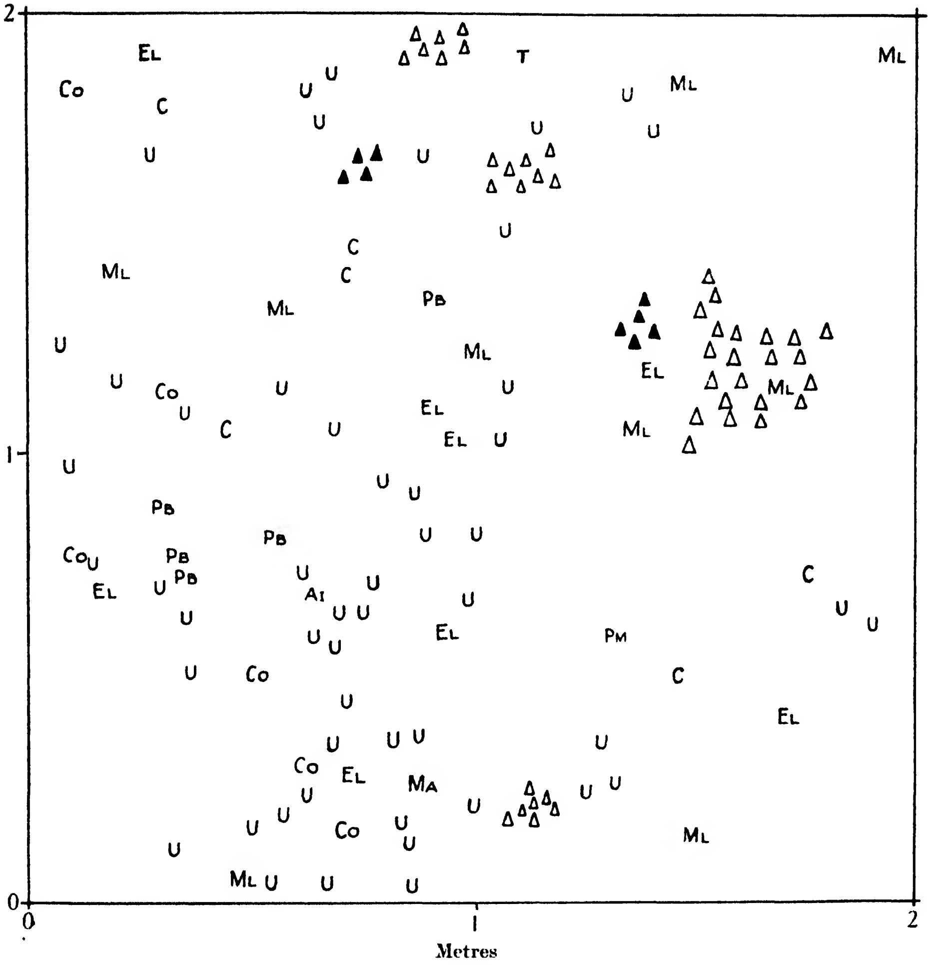


Fig. 4. Quadrat 4 sq. metres (2 m. × 2 m.) in sample plot no. 1, showing distribution of ground flora including seedlings and young plants not exceeding 50 cm. high.

Explanation of symbols

Seedlings and young plants

Ai	Allophylus integrifolius Bl.	Pb	Psathura borbonica Gmel.
Co	Conopharyngia mauritiana (Poir.) R.E.V.	Pm	Psathura myrtifolia A. Rich.
Ei	Erythroxylon laurifolium Lam.	Ts	Tambourissa Sieberi DC.
Ma	Molinaea arborea Gmel.	U	Unidentified
Mi	Mallotus integrifolius Muell.-Arg.		

Herbaceous species

Δ	Pilea urticifolia Blume	▲	Pilea verbascifolia Wedd.

Table 5. *Comparative frequency of species in three phases of the upland sere*

	Individuals in 1000 sq. metres		
Species	(1) Heath associes (Petrin)	(2) *Sideroxylon* consocies (Perrier)	(3) Upland Climax Forest (Macabé) sample plot no. 1
Philippia abietina Klotzsch	890	—	—
Phylica mauritiana Bojer	304	—	—
Helichrysum yuccifolium Lam.	93	—	—
Tambourissa sp. (Tx)	44	—	—
Croton fothergillifolius Baill.	8	—	—
Trochetia Blackburniana Bojer	5	×	—
Embelia concinna Baker	3	—	—
Dodonaea viscosa Linn.	1	×	—
Haronga madagascariensis Choisy	1	×	×
Sideroxylon puberulum A. DC.	106	63	×
Psiadia trinervia Willd.	91	15	—
Olea lancea Lam.	62	46	×
Casaeria fasciculata Bojer ex Baker	46	38	×
Sideroxylon Bojerianum A. DC.	42	56	×
Faujasia flexuosa Benth.	2	25	×
Badula sp.	1	1	×
Tambourissa peltata Baker	1	2	×
Doratoxylon mauritianum Thouars	1	66	×
Aphloia theiformis Benth.	366	170	154
Antirrhoea verticillata DC.	33	252	1
Eugenia glomerata Lam. (including subspecies)	31	5	187
Phyllanthus phillyreifolius Poir.	16	3	1
Molinaea arborea Gmel.	15	54	19
Ochna mauritiana Lam.	12	1	1
Gaertnera psychotrioides Baker	11	56	15
Labourdonnaisia sp. (Lg)	10	18	20
Nuxia verticillata Lam.	6	9	35
Erythroxylon laurifolium Lam.	3	135	85
Eugenia orbiculata Lam.	1	660	71
Ocotea cupularis Cordem.	1	3	1
Homalium paniculatum Benth.	—	96	×
Ixora parviflora Lam.	—	87	×
Grangeria borbonica Lam.	—	33	×
Vepris paniculata Engl.	—	32	×
Psathura terniflora A. Rich.	—	30	×
Pittosporum Senecia Putterl.	—	27	—
Pandanus sp.	—	24	—
Danais fragrans Comm.	—	18	—
Eugenia rampans Baker	—	9	—
Geniostoma pedunculatum Bojer ex Baker	—	8	×
Rutidea coriacea Baker	—	8	×
Diospyros pterocalyx Bojer ex Baker	—	7	×
Evodia sp. (E_{32})	—	5	—
Dracaena sp.	—	5	×
Ficus mauritiana Lam.	—	5	×
Diospyros tesselaria Poir.	—	4	×
Stillingia lineata Muell.-Arg.	—	4	×
Calophyllum Inophyllum L. var. Tacamaha (Willd.) R.E.V.	—	3	×
Antidesma Boutoni Baker	—	2	—
Gouania tiliifolia Lam.	—	2	—
Apodytes mauritiana Planch.	—	1	×
Evodia elaeodendroides Baker	—	1	×
Gaertnera sp.	—	1	—
Hugonia tomentosa Cav.	—	1	—
Pseudannona amplexicaulis Safford	—	1	—
Pyrostria macrophylla A. Rich.?	—	1	—
Securinega durissima Gmel.	—	490	1
Erythrospermum mauritianum Lam.	—	387	147
Acalypha colorata Spreng.	—	123	1
Cnestis glabra Lam.	—	75	48
Antidesma longifolium Bojer	—	71	1
Ludia sessiliflora Lam.	—	66	2
Mimusops maxima (Poir.) R.E.V.	—	60	2

Table 5 (*continued*)

Species	Individuals in 1000 sq. metres: (1) Heath associes (Petrin)	(2) *Sideroxylon* consocies (Perrier)	(3) Upland Climax Forest (Macabé) sample plot no. 1
Pleurostylia leucocarpa Baker	—	56	1
Memecylon trinerve DC.	—	51	3
Conopharyngia mauritiana (Poir.) R.E.V.	—	50	136
Geniostoma borbonicum Spreng.	—	48	1
Ochrosia parviflora G. Don	—	36	2
Elaeodendron orientale Jacq.	—	34	16
Bertiera Zaluzania Comm.	—	31	3
Colea mauritiana Bojer	—	24	1
Mallotus integrifolius Muell.-Arg.	—	22	3
Tambourissa amplifolia DC.	—	16	1
Memecylon angulatum Reich.	—	16	26
Eugenia venosa Lam.	—	14	50
" Bois Caf-Caf"	—	14	54
Scutia Commersoni Brongn.	—	14	1
Fernelia buxifolia Lam.	—	9	4
Mimusops petiolaris Dubard?	—	8	3
Eugenia sp. (Ej)	—	6	1
Molinaea macrantha Radl.	—	5	1
Ficus terebrata Willd.?	—	4	2
Xylopia Richardi Boiv.	—	4	3
Memecylon cordatum Desv.	—	3	1
Molinaea cupanioides Radl.	—	3	1
Diospyros sp. (Dx)	—	2	1
Allophylus integrifolius Bl.	—	2	4
Antidesma madagascariense Lam.	—	1	1
Chasalia capitata DC.		—	286
Psathura borbonica Gmel.	—	—	128
Psathura myrtifolia A. Rich.	—	—	105
Ixora sp. (Is)	—	—	32
Tambourissa pedicellata Baker	—	—	28
Eugenia cymosa Lam.	—	—	14
Tambourissa Sieberi DC.	—	—	13
Erythrospermum amplifolium Thouars	—	—	9
Psathura terniflora A. Rich.? (P_{21})	—	—	9
Chasalia grandifolia DC.	—	—	8
Coffea macrocarpa A. Rich.	—	—	8
Clematis mauritiana Lam.	—	—	6
Canarium mauritianum Bl.	—	—	5
Tambourissa elliptica (Tul.) DC.?	—	—	4
Psiloxylon mauritianum Baill.	—	—	3
Toddalia aculeata Pers.	—	—	3
Calvaria major Gaertn.	—	—	2
Quivisia oppositifolia Cav.	—	—	2
Claoxylon linostachys Baill.	—	—	1
Diospyros nodosa Poir.? (D_9)	—	—	1
Evodia sp.	—	—	1
Gaertnera sp.	—	—	1
Hugonia serrata Lam.	—	—	1
Leea Sambucina Willd.	—	—	1
Mussaenda Landia Lam.	—	—	1
Oncostemon latifolium Mez	—	—	1
Totals	2206	3838	1785

SUMMARY

No. of species:

(*a*) In heath associes only	9
(*b*) In heath associes and *Sideroxylon* consocies	9
(*c*) In heath associes, *Sideroxylon* consocies and climax forest	12
(*d*) In *Sideroxylon* consocies	26
(*e*) In *Sideroxylon* consocies and climax forest	32
(*f*) In climax forest	26
Total no. of species	114

DEVELOPMENT

An account of the seral relationships between the primary plant communities of the uplands and the development of the forest has already been given in the first paper of this series (Vaughan & Wiehe, 1937). During the course of the present investigation, however, some further quantitative data have become available. The communities which have been studied in further detail are the *Philippia* heath associes and the *Sideroxylon* thicket consocies, in both of which 1000 sq. metre quadrats have been charted so that the results could be compared with those of sample plot no. 1 in the upland climax forest. All the plants recorded are either phanerophytes or rope lianes. They are arranged in numerical order (Table 5), those belonging to the heath associes being placed first, then the species of the *Sideroxylon* consocies, and finally those of the upland climax forest. A cross indicates that the particular species is known to occur in the community, but was not actually found in the quadrats.

The interest of the *Philippia* heath associes lies in the fact that it probably represents the initial stage in the development of the climax forest, and there is no doubt that it formerly covered a very much larger area than the few square kilometres which it occupies to-day. Its component species are extremely well adapted to meet the peculiar conditions which prevail on an unweathered lava subjected to violent rains and comparatively long periods of tropical sun.

This was very probably the type of vegetation which first colonized the uplands when volcanic activity subsided sufficiently to allow plant life to appear. It is important to note, therefore, that the climax forest has developed from what was essentially a phanerophytic community, and that grasses and herbaceous plants have played an altogether insignificant part in its evolution.

A notable feature of the heath associes is the marked dominance of three species peculiar to it: *Philippia abietina* (Ericaceae), *Phylica mauritiana* (Rhamnaceae) and *Helichrysum yuccifolium* (Compositae). These species form a semi-open nanophanerophyte stratum 1–3 m. high underneath which a ground flora of *Gleichenia*, *Lycopodium* and *Cladonia* spp. frequently arises. In later stages of the sere low trees of *Sideroxylon puberulum* with spreading rather flat-topped crowns form an open canopy 5–7 m. high. Under the shade of the *Sideroxylon* other species are able to germinate and the sere gradually passes into a *Sideroxylon* consocies.

It will be noticed that twenty-one species of the climax forest are already present in the heath associes, four of these being species, including *Sideroxylon*, which belong to the top canopy of large trees.

The family dominance table for the heath associes (Table 6) may be compared with that already given for the upland climax forest (Table 4).

Table 6. *Family dominance. Relation between family/species and family/individuals for all phanerophytes recorded in* 1000 *sq. metres* (50 *m.* × 20 *m.*) *of the heath associes*

Family	Species	%	Individuals	%
Compositae	3	10·0	186	8·54
Sapotaceae	3	10·0	158	7·17
Sapindaceae	3	10·0	17	0·77
Monimiaceae	2	6·7	45	2·04
Rubiaceae			44	1·99
Myrtaceae			32	1·45
Euphorbiaceae			24	1·09
Myrsinaceae			4	0·18
Ericaceae	1	3·3	890	40·3
Flacourtiaceae			366	16·6
Rhamnaceae			304	13·8
Oleaceae			62	2·86
Samydaceae			46	2·06
Ochnaceae			12	0·55
Loganiaceae			6	0·27
Sterculiaceae			5	0·23
Linaceae			3	0·14
Hypericaceae			1	0·05
Lauraceae			1	0·05
Totals	30	—	2206	—
Families 19				

The *Sideroxylon* consocies may be regarded as a subclimax of the upland forest. The ultimate stratification of the upland forest is already discernible in this consocies, and a very large number of species are common to both communities.

The name *Sideroxylon* consocies is derived from the nearly exclusive dominance in the top canopy of two closely allied species of *Sideroxylon*—*S. Bojerianum* and *S. puberulum*. These two species form an open canopy about 8–10 m. high, under which is a dense closed stratum of very complex floristic composition comprising about eighty species and over 3500 individuals of woody plants in 1000 sq. metres. Beneath this, again, there is a thinly populated stratum of herbaceous plants and nanophanerophytes. The most important feature of the *Sideroxylon* consocies is the extreme density of the second stratum with the consequent exclusion of direct sunlight from the forest floor. This brings about a fundamental change in the environmental conditions, and enables the growth and development of the third and fourth strata species and the characteristic ground flora of the climax forest to take place.

In conclusion, species/area curves for the three communities have been prepared (Fig. 5). In order to obtain the figures (Table 7) on which the curves are based, a large number of quadrats of different areas were thrown at random within the 1000 sq. metre plots; the actual number of quadrats examined for each area is given in column 2 of Table 7.

It will be seen that, in the case of the heath associes, the community rapidly becomes saturated, and comparatively small quadrats are sufficient to obtain some reliable ecological data. The curve for the *Sideroxylon* consocies illustrates in a striking manner the rapid influx of species which takes place when the *Sideroxylon* canopy is formed. In the climax forest the population is more widely dispersed and stocking less dense, a feature which is borne out by the continued upward trend of the curve.

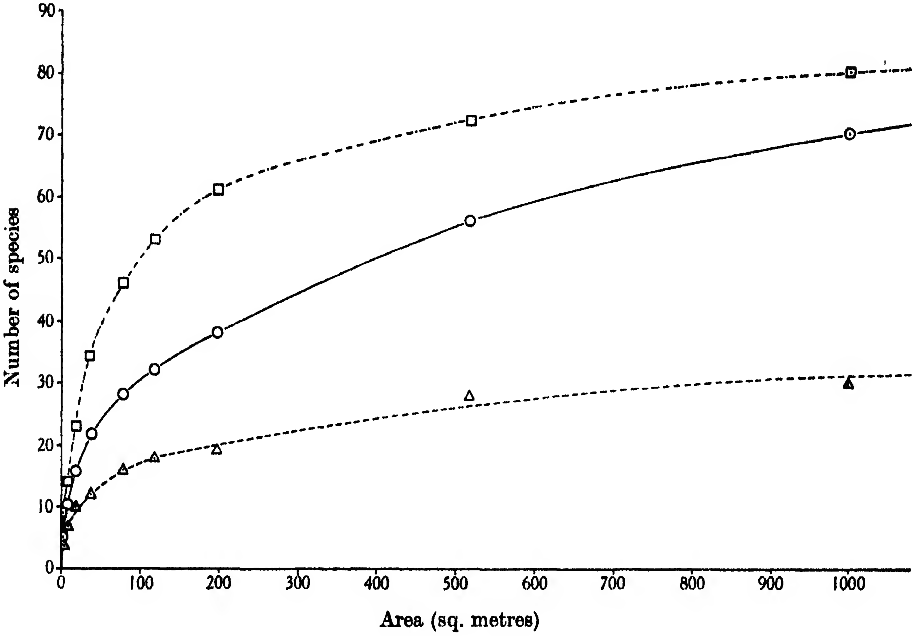


Fig. 5. Species/area curves for phanerophytes in (1) heath associes (triangles), (2) *Sideroxylon* consocies (squares), and (3) the upland climax forest (circles).

Table 7

Area in sq. metres	No. of quadrats examined	Mean number of species in given area: (1) Heath associes	(2) *Sideroxylon* consocies	(3) Climax forest: sample plot no. 1
2	150	—	6	3
4	100	4	9	5
10	50	6	16	10
20	25	10	23	15
40	25	12	34	22
80	12	16	46	28
120	10	18	53	32
200	5	19	61	38
520	2	28	72	56
1000	1	30	79	70

ALPHABETICAL KEY TO SYMBOLS

(For vernacular name, family, distribution and life form, see Appendix, below)

Ac	Acalypha colorata Spreng.
Ai	Allophylus integrifolius Bl.
Al	Antidesma longifolium Bojer
Ao	Antidesma madagascariense Lam.
At	Aphloia theiformis Benn.
Av	Antirrhoea verticillata DC.
Bz	Bertiera Zaluzania Comm. ex Gaertn.
C	"Bois Caf-Caf"
Cc	Chasalia capitata DC.
Cg	Cnestis glabra Lam.
Cj	Claoxylon linostachys Baill.
Cl	Canarium mauritianum Bl.
Cm	Colea mauritiana Bojer
Co	Conopharyngia mauritiana (Poir.) R.E.V.
Cq	Coffea macrocarpa A. Rich.
Cv	Calvaria major Gaertn.
Cw	Chasalia grandifolia DC.?
Cz	Clematis mauritiana Lam.
Dx	Diospyros sp.
D_9	Diospyros sp.
Ea	Erythrospermum amplifolium Thouars
Ec	Eugenia orbiculata Lam.
Eg	Eugenia glomerata Lam.
Ej	Eugenia sp.
El	Erythroxylon laurifolium Lam.
Em	Erythrospermum mauritianum Baker
Eo	Elaeodendron orientale Jacq.
Ev	Eugenia venosa Lam.
E_{20}	Eugenia glomerata Lam. var.
E_{21}	Eugenia cymosa Lam.
E_{22}	Evodia sp.
F	Ficus sp.
Fb	Fernelia buxifolia Lam.
Gb	Geniostoma borbonicum Spreng.
Gp	Gaertnera psychotrioides Baker
H	Gaertnera sp.?
Ht	Hugonia serrata Lam.
Is	Ixora sp.
Lc	Leea sambucina Willd.
Lg	Labourdonnaisia sp.
Ls	Ludia sessiliflora Lam.
M	Mussaenda Landia Poir.?
Ma	Molinaea arborea Gmel.
Mc	Memecylon cordatum Desv.
Mi	Mimusops petiolaris Dubard?
Ml	Mallotus integrifolius Muell.-Arg.
Mm	Mimusops maxima (Poir.) R.E.V.
Mn	Memecylon angulatum Reich.
Mo	Molinaea macrantha Radl.
Ms	Molinaea cupanioides Radl.
Mt	Memecylon trinerve DC.
Nv	Nuxia verticillata Lam.
Ob	Ochrosia parviflora G. Don
Oc	Ocotea cupularis Cordem.
Om	Ochna mauritiana Lam.
Os	Oncostemon latifolium Mez
p	Pleurostylia sp.?
Pb	Psathura borbonica Gmel.
Pm	Psathura myrtifolia A. Rich.
Pp	Phyllanthus phillyreifolius Poir.
Px	Psiloxylon mauritianum Baill.
P_{21}	Psathura terniflora A. Rich.?
Q	Quivisia oppositifolia Cav.
Sc	Scutia Commersoni Brongn.
Sd	Securinega durissima Gmel.
Ta	Tambourissa amplifolia DC.
To	Toddalia aculeata Pers.
Tp	Tambourissa elliptica (Tul.) DC.?
Ts	Tambourissa Sieberi DC.
T_2	Tambourissa pedicellata Baker
Xv	Xylopia Richardi Boiv.
†	Dead, but trunk still standing.

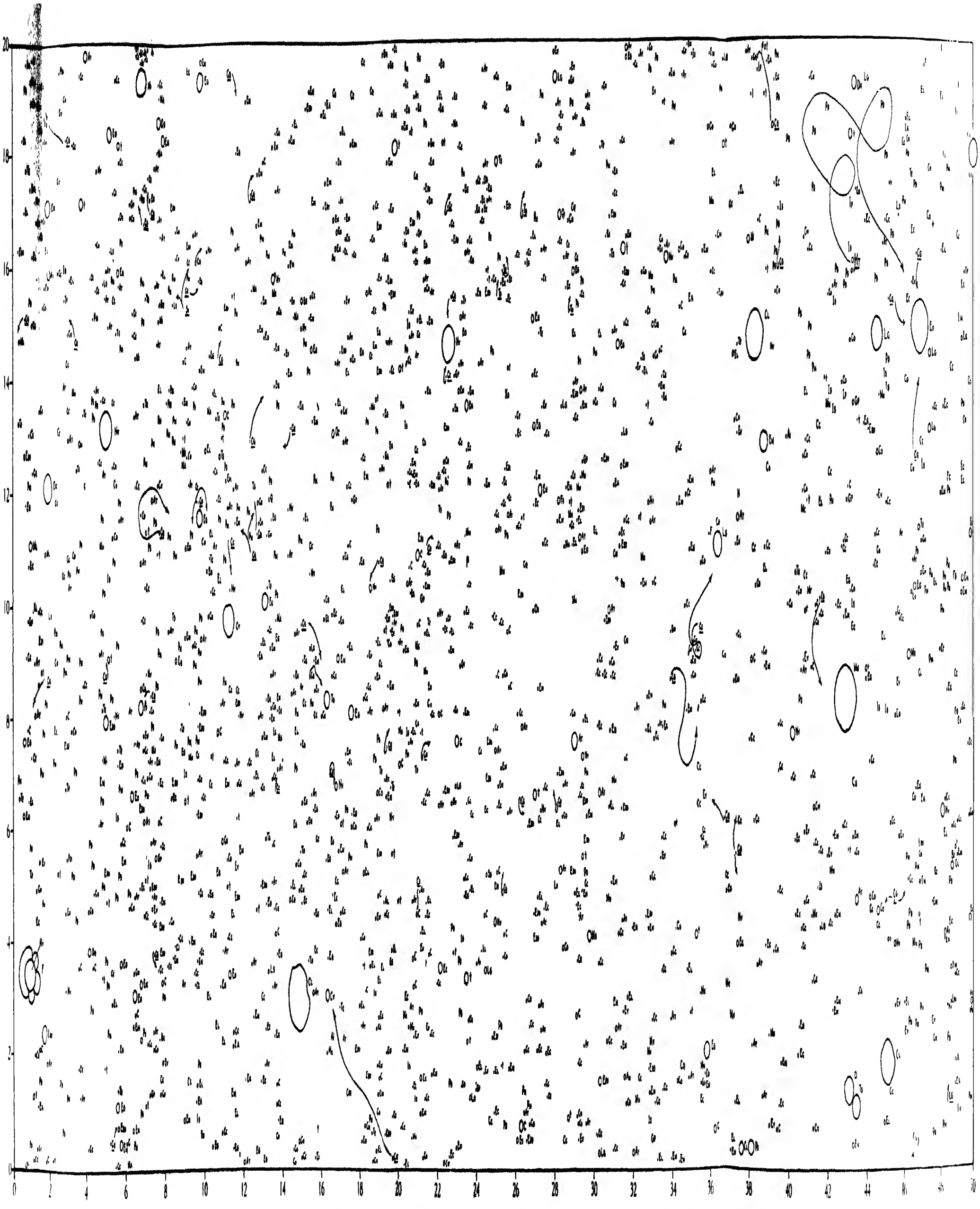


Fig. 6 The upland climax forest of Mauritius (Crown Land Macabé), sample plot no. 1. The chart represents an area of 1000 sq. metres (50 m. × 20 m.). All phanerophytes 50 cm. high and above, or 1 cm. in diameter and over, and some lianes are shown. Individuals with a diameter of 5 cm. and over are drawn to scale, those below 5 cm. are represented by their symbols only. The lianes are underlined and the approximate direction of their stems up to 2 m. high is shown by arrows.

Face page 150

THE FORMATION

Many descriptions of tropical woody vegetation are now available, but there is still a scarcity of statistical data essential for an ecological classification of tropical forests. In consequence it is difficult to fit the upland climax forest of Mauritius into any existing scheme of classification. In the habit and distribution of the smaller woody plants the Mauritius formation resembles that of the Sinharaja forest of Ceylon described by Baker (1938), but in the latter, stratification is less evident, and the whole forest is on a much grander scale. Further, leaves with drip tips, so often described by observers in tropical evergreen forests, are not a conspicuous feature of Mauritius trees.

A character in which the Mauritius upland forest seems to be peculiar is the remarkable number of individuals, amounting to over seventeen hundred, of 10 cm. diameter and over per hectare. The general size and height of all species, however, seems less than those in corresponding strata of typical evergreen tropical forest.

No doubt these divergences are due in the first place to the altitude and higher latitude with consequent reduction in temperature, but the effect of long isolation in producing anomalous features must not be overlooked.

On the whole the most satisfactory formation to which this forest may be referred is the "subtropical Rain-forest of the lower montane regions in the tropics", Schimper (1903, p. 285), or the "Tropical Lower-montane Evergreen Rain-forest" of Burtt Davy (1938, p. 31), regarded by him as a subformation of the Tropical Lowland Evergreen Rain-forest.

It has been thought desirable, as far as the subject-matter of this paper allows, to answer the questionnaire proposed by Burtt Davy (1938, p. 79). The marginal numbers and letters are the same as those used in his original paper. Further, an attempt is made in Table 8 below to draw up a comparative statement between the upland forest of Mauritius and those of three tropical regions, Southern Nigeria, Sarawak and British Guiana, from which important data are now available through the work of Davis & Richards (1933–34) and Richards (1936, 1939).

I. *Composition*

The following abbreviations are used in this table: A (abundant), C (common), L (local), R (rare), and O (absent)

		A	C	L	R	O
1.	Conifers	.	.	.	.	×
2.	Dicotyledons ("broad-leaved" trees)	×	.	.	.	.
3*a*.	Monocotyledons					
(*a*)	Palms	.	.	.	×	.
(*b*)	Screw-pines	×	.	.	.	.
(*c*)	Woody Liliaceae (e.g. *Dracaena*)	.	.	×	.	.
(*d*)	Bamboos	.	.	.	.	×
(*e*)	Herbaceous grasses	.	.	.	×	.
(*f*)	Sedges	×	.	.	.	.
(*g*)	Other herbaceous plants	.	.	.	×	.
3*b*.	Flowerless plants					
(*h*)	Ferns (epiphytic)	×	.	.	.	.
(*i*)	Mosses, liverworts or lichens (epiphytic)	×	.	.	.	.
4.	Lianes	×	.	.	.	.
5.	Epiphytes	×	.	.	.	.

6. The herbaceous ground vegetation is composed mainly of Urticaceae and Orchidaceae; mosses and ferns rare. Note: screw-pines and sedges are abundant only in the early stages of development of the climax forest.

II. *Physiognomy*

		A	C	L	R	O
7. (*j*)	Buttresses: in top strata species	×	.	.	.	.
	in other species	.	.	.	×	.
(*k*)	Stilt-roots	.	.	.	.	.
(*l*)	Knee-roots	.	.	.	.	×
(*m*)	Pneumatophores	.	.	.	.	×
(*n*)	Strangling figs	.	.	×	.	.
(*o*)	Trees or shrubs with thin (herbaceous or chartaceous) leaves	.	.	.	.	×
(*p*)	Trees or shrubs with thin (leathery coriaceous) leaves	.	×	.	.	.
(*q*)	Trees or shrubs with hard firm (sclerophyllous) leaves	.	×	.	.	.
(*r*)	Trees or shrubs with succulent leaves	.	.	.	.	×
(*s*)	Trees or shrubs with large leaves	.	×	.	.	.
(*t*)	Trees or shrubs with small leaves	.	×	.	.	.
(*u*)	Trees or shrubs with compound leaves	.	.	.	×	.
(*v*)	Trees or shrubs with drip-tip (long-pointed) leaves	.	.	.	×	.
(*w*)	Trees or shrubs with thorns or prickles	.	.	.	×	.
(*x*)	Evergreen trees	×	.	.	.	.
(*y*)	Evergreen shrubs	×	.	.	.	.
(*z*)	Deciduous trees or shrubs	.	.	.	×	.

8. Three tree and one shrub strata are recognized.

9. Top stratum above 15 m.
Second tree stratum 8–15 m.
Third tree stratum 2–8 m.
Shrub stratum 0·5–2 m.

10. The canopy is closed in the second stratum from 8 to 15 m.

11. Lianes materially assist in the closure of canopy referred to in 10.

12, 13. Roof of second stratum more or less even, with the crown of the top stratum standing clear.

17. Species are not gregarious; a notable exception is Calophyllum Inophyllum L. var. Tacamaha (Willd.) R.E.V.

III. *Periodicity* ("*Phenology*")

21. The flowering season for most species is just before or during the summer rains.

IV. *Biotic data of the community*

Queries not applicable or not sufficient data yet available.

V. *Statistical data of the community*

34. Number of trees per acre.
A. 1–2 ft. girth at breast height (10–20 cm. diameter) = 542.
B. 2–4 ft. girth at breast height (20–40 cm. diameter) = 122.
C. 4–8 ft. girth at breast height (40–80 cm. diameter) = 26.
D. Exceeding 8 ft. girth at breast height (80 cm. diameter) = 1–2.

35. Number of different species per hectare 1 ft. girth breast height (10 cm. diameter) and above equals 52.

36. For number of individuals of each species per hectare 1 ft. girth breast height (10 cm. diameter) and above see Table 1, p. 132.

38. In the top stratum of big trees the family Sapotaceae is dominant.

39. Present area covered by the community about 7 sq. miles, original area probably 150 to 200 sq. miles.

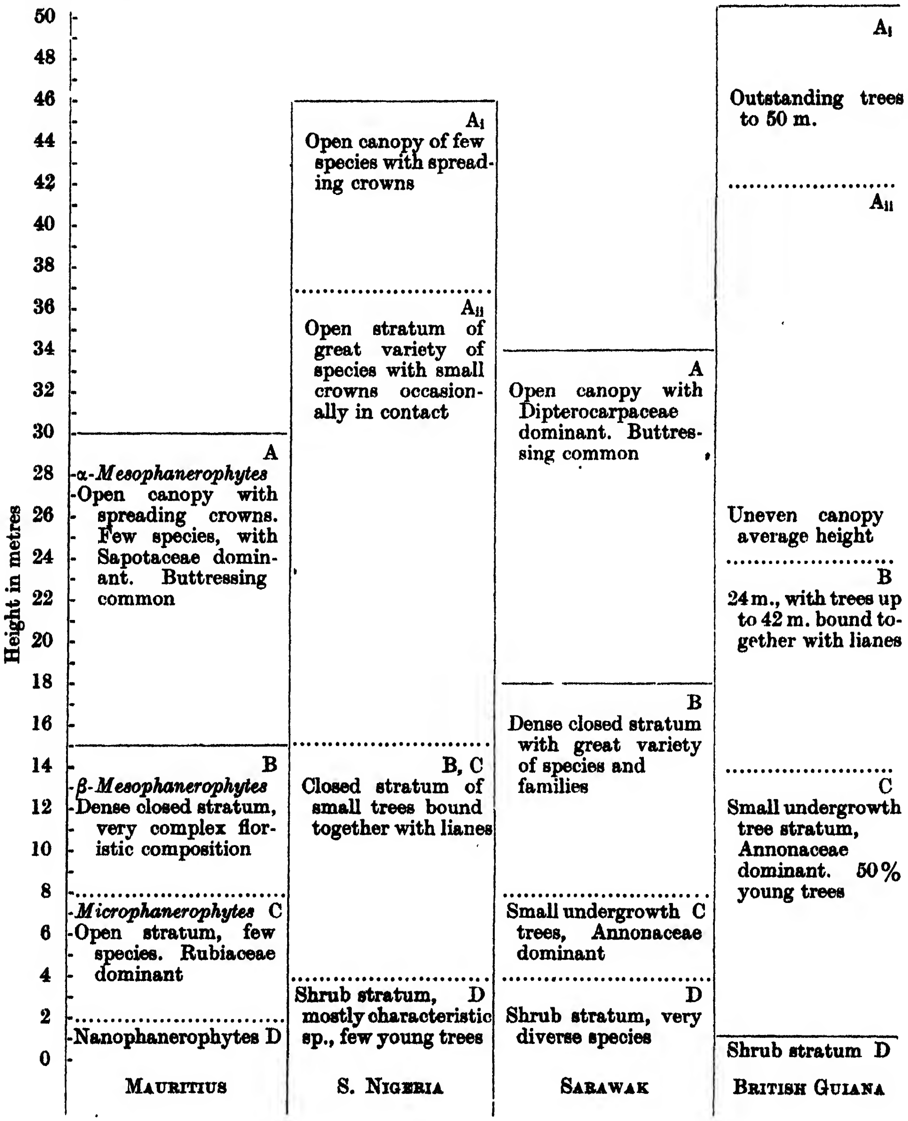
Table 8. *Comparative data from rain forest in four regions*

1. Locality	I. Mauritius: Crown Land Macabé		II. S. Nigeria: Nikrowa (rainfall: Akilla)		III. Sarawak: Mt. Dulit (Mixed Forest)		IV. British Guiana: Moraballi Creek (Mixed Forest)	
2. Latitude	20° 24′ S.		c. 6° 10′		3° 19′ N.		6° 11′ N.	
3. Longitude	57° 27′ S.		c. 5° 20′		114° 17′ E.		58° 40′ W.	
4. Altitude	1800 ft. (550 m.)		Near sea-level		Under 1000 ft. (E. 300 m.)		164–328 ft. (50–100 m.)	
5. Rainfall (mm.) and rain days								
Jan.	525·4	22	28	1·4	—	—	—	17
Feb.	403·6	23	35	2·9	—	—	—	12
March	436·2	24	96	7·6	—	—	—	13
April	438·4	25	180	9·2	—	—	—	10
May	296·1	23	196	12·8	—	—	—	20
June	184·8	21	407	18·1	—	—	—	24
July	232·22	26	419	16·9	—	—	—	22
Aug.	291·7	25	134	12·5	—	—	—	18
Sept.	104·6	19	252	18·3	—	—	—	15
Oct.	127·4	17	242	16·2	—	—	—	16
Nov.	240·8	15	80	7·9	—	—	—	15
Dec.	510·7	20	11	1·4	—	—	—	23
Year	3791·9	260	2080	125·2	3000–4500	—	2670	205
6. Distribution of rain	Heavy summer rains, rarely a month with less than 100 mm.		Dry season very marked, 2–3 months with less than 50 mm.		Very slight seasonal range, with even rainfall. No month with less than 100 mm.		Two wet seasons: no month with less than 100 mm.	
7. Relative humidity mean (%)	87		—		—		—	
8. Temperature (° C.)								
Mean max.	22·9°		31°		—		—	
Mean min.	17·4°		18–24°		—		—	
Mean annual	19·9°		25·5°		27°		25·9°	
Mean daily range	5·5°		3°		6–8°		—	
9. Sunshine (hr.)	6·95		—		6·0		5·5	
10. Soils	Immature laterized soil on highly ferruginous lava		Tropical Red Earth		Very uniform heavy, sticky bright yellow loam		Mostly tropical red earth	
Soil *p*H	5·4		5·0–6·2		4·55		4·3–4·7	
No. of individuals per hectare								
10 cm. diameter and over	1710		390		—		432	
20 cm. diameter and over	331		213		184		222	
41 cm. diameter and over	60		47		44		60	
No. of species on plot of 1·418 hectares								
10 cm. diameter and over	*52		70		—		91	
20 cm. diameter and over	*33		51		98		57	
41 cm. diameter and over	*11		31		32		31	
Most abundant species on plot of 1·418 hectares (%)								
10 cm. diameter and over	*18		30		—		11	
20 cm. diameter and over	*19		35		5		13	
41 cm. diameter and over	*25		14		10		16	

* For plots of *one* hectare only.

Stratification

A comparative scheme is attempted below to illustrate stratification in the four regions. A continuous horizontal line represents a definite break between strata, a dotted line indicates a more or less gradual transition. Capital letters are assigned to what appear to be corresponding zones or strata.



Mauritius

A — *α-Mesophanerophytes*. Open canopy with spreading crowns. Few species, with Sapotaceae dominant. Buttressing common

B — *β-Mesophanerophytes*. Dense closed stratum, very complex floristic composition

C — *Microphanerophytes*. Open stratum, few species. Rubiaceae dominant

D — Nanophanerophytes

S. Nigeria

A I — Open canopy of few species with spreading crowns

A II — Open stratum of great variety of species with small crowns occasionally in contact

B, C — Closed stratum of small trees bound together with lianes

D — Shrub stratum, mostly characteristic sp., few young trees

Sarawak

A — Open canopy with Dipterocarpaceae dominant. Buttressing common

B — Dense closed stratum with great variety of species and families

C — Small undergrowth trees, Annonaceae dominant

D — Shrub stratum, very diverse species

British Guiana

A I — Outstanding trees to 50 m.

A II

B — Uneven canopy average height 24 m., with trees up to 42 m. bound together with lianes

C — Small undergrowth tree stratum, Annonaceae dominant. 50% young trees

D — Shrub stratum

SUMMARY

The upland climax forest is now reduced to an area of about 18 sq. km. in isolated blocks, the least altered of which is that in Crown Land Macabé situated above the Black River Gorges at an altitude of 550 m. above sea-level. The climate and soils are briefly described, and an account is given of the methods being used to obtain some meteorological data for the internal climate of the forest.

The structure of the forest is studied firstly by means of ten plots of 1000 sq. metres, each taken at random; all phanerophytes 10 cm. diameter and above are measured and sorted into fourteen diameter classes. From the data obtained size-class frequency curves for the whole population and for certain species are drawn, and the abnormalities shown by some species of large trees are discussed. The number of individuals per hectare 10 cm. diameter and above is found to be 1710 and the total phanerophytic population per hectare is estimated at 208,510.

Stratification and floristic composition are studied in more detail by means of a 1000 sq. metre plot in which all species 50 cm. high and above, or 1 cm. in diameter and over, are charted to scale.

It is found that the woody plants may be grouped into four distinct strata: α-mesophanerophytes, above 15 m.; β-mesophanerophytes, 8–15 m.; microphanerophytes, 2–8 m.; and nanophanerophytes, 0·5–2 m. high. The family Sapotaceae is dominant in the open or top stratum of large trees which comprises about twelve species. The second closed stratum is composed of an extremely complex and varied assemblage of small trees, underneath which the third and fourth open strata of under-trees and shrubs develop.

The ground flora is investigated by means of small quadrats of 1–4 sq. metres, the mean number of seedlings being 19·08 per sq. metre. Herbaceous plants are few and scattered but great variety is observed in life forms; the families Orchidaceae and Urticaceae are dominant. Ferns, mosses and hepatics are very rare.

The development of the forest is studied by 1000 sq. metre plots laid down at different stages of the sere, and species/area curves are prepared from the data obtained. The climax forest is shown to have developed from a phanerophytic heath community.

The status of the forest is discussed, and its general structure compared with tropical forests in British Guiana, Sarawak and Southern Nigeria. The formation is probably akin to the Tropical Lower-Montane Evergreen Rainforest of Burtt Davy (1938).

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APPENDIX

Botanical and vernacular name, ecological symbol, family, distribution, and life form of all indigenous species recorded in the text

ABBREVIATIONS

(i) Distribution	
C.	Ceylon
E.	Endemic
M.	Madagascar
Mal.	Malaya
O.W.T.	Old World Tropics
P.	Polynesia
R.	Réunion
Rod.	Rodriguez
Sey.	Seychelles

(ii) Life forms	
Mα	α-Mesophanerophyte
Mβ	β-Mesophanerophyte
Mi.	Microphanerophyte
N.	Nanophanerophyte
H.P.	Herbaceous phanerophyte
He.	Hemicryptophyte

Botanical name	Ecological symbol	Vernacular name	Family	Distribution	Life form
Acalypla colorata Spreng.	Ac	Bois queue de rat	Euphorbiaceae	M., Co.	N.
Allophylus integrifolius Bl.	Ai	Bois trois feuilles Bois merle	Sapindaceae	S.E. Asia?	Mβ
Antidesma Boutoni Baker	—	—	Euphorbiaceae	E.	Mi.
Antidesma longifolium Bojer ex Baker	Al	—	Euphorbiaceae	E.	Mβ
Antidesma madagascariense Lam.	Ao	Bois Bigaignon bâtard	Euphorbiaceae	M., R.	Mβ
Antirrhoea verticillata DC.	Av	Bois Lousteau	Rubiaceae	R.	Mβ
Aphloia theiformis Benn.	At	Fandamane	Flacourtiaceae	M., R., Rod.	Mβ
Apodytes mauritiana Planch.	—	Bois bleu	Icacinaceae	E.	Mβ
Badula insularis DC.	—	Bois pintade	Myrsinaceae	R.	Mi.
Bertiera Zaluzania Comm.	Bz	Bois bleu	Rubiaceae	R.	Mi.
Calanthe sylvatica Lindl.	—	—	Orchidaceae	R.	Hc.
Calophyllum Inophyllum L. var. Tacamaha (Willd.) R.E.V.	Cl	Tatamaka	Guttiferae	Mal., P., Australia	Mα
Calophyllum parviflorum Bojer ex Baker	—	Tatamaka à petites feuilles	Guttiferae	E.	Mβ
Calvaria major Gaertn.	Cv	Tambalocoque	Sapotaceae	E.	Mα
Casaeria fasciculata Bojer ex Baker	Cf	Bois banane	Samydaceae	E.?	Mβ
Chasalia capitata DC.	Cc	Bois corail	Rubiaceae	E.	Mi.
Chasalia grandifolia DC.?	Cw	Bois corail	Rubiaceae	E.	Mi.
Claoxylon linostachys Baill.	Cj	—	Euphorbiaceae	E.	Mi.?
Clematis mauritiana Lam.	Cz	Vigne vierge	Ranunculaceae	M., R.	Liane
Cnestis glabra Lam.	Cg	Mort aux rats	Connaraceae	R.	Liane
Coffea macrocarpa A. Rich.	Cq	—	Rubiaceae	E.	Mi.
Colea mauritiana Bojer ex Baker	Cm	Bois margoze	Bignoniaceae	E.	Mi.
Conopharyngia mauritiana (Poir.) R.E.V.	Co	Bois de lait	Apocynaceae	R.	Mβ
Croton fothergillifolius Baill.	—	—	Euphorbiaceae	E.	N.
Danais fragrans Comm.	—	Liane jaune	Rubiaceae	M.?	Liane
Diospyros nodosa Poir.?	D_9	Bois d'ébène marbré à petites feuilles	Ebenaceae	E.	Mβ
Diospyros pterocalyx Bojer ex Baker	—	Bois d'ébène marbré	Ebenaceae	E.	Mβ
Diospyros tesselaria Poir.	—	Bois d'ébène noir	Ebenaceae	E.	Mβ
Diospyros sp.	D_{10}	—	Ebenaceae	E.	Mβ
Diospyros sp.	Dx	Bois d'ébène marbré à grosses feuilles	Ebenaceae	E.	Mβ
Dispersis oppositifolia (Thouars) Smith	—	—	Orchidaceae	R.	Hc.
Dispersis tripetaloides (Thouars) Lindl.	—	—	Orchidaceae	R.	Hc.
Dodonaea viscosa L.	—	Bois de reinette	Sapindaceae	Tropics	Mi.
Doratoxylon mauritianum Thouars	—	Bois de sagaie rouge	Sapindaceae	R.	Mβ
Dracaena sp.	—	Bois chandelle	Liliaceae	?	N.
Elaeodendron orientale Jacq.	Eo	Bois d'olive	Celastraceae	M., R.	Mα
Erythrospermum amplifolium Thouars	Ea	—	Flacourtiaceae	E.	Mβ
Erythrospermum mauritianum Baker	Em	Bois manioc	Flacourtiaceae	M., R.	Mβ

Erythoxylon laurifolium Lam.	El	Bois de ronde	Linaceae	E.	Mβ
Eugenia cymosa Lam.	E_{21}	—	Myrtaceae	E.	Mβ
Eugenia glomerata Lam.	E_{20} Eg	Bois pomme	Myrtaceae	M., R.	Mα
Eugenia orbiculata Lam.	Ec	Bois clou	Myrtaceae	R.	Mβ
Eugenia rampans Baker	—	—	Myrtaceae	E.?	Liane?
Eugenia venosa Lam.	Ev	—	Myrtaceae	M.	Mβ
Eugenia sp.	Ej	Bois pomme jamalac	Myrtaceae	E.?	Mβ
Eugenia sp.	E_{26}	—	Myrtaceae	E.?	Mβ
Evodia elaeodendroides Baker	—	—	Rutaceae	E.?	Mi.?
Evodia sp.	E_{32}	—	Rutaceae	E.?	Mi.
Faujasia flexuosa Benth.	—	Bois cassant	Compositae	M., R.	H.P.
Fernelia buxifolia Lam.	Fb	Bois de buis	Rubiaceae	R.	Mβ
Ficus terebrata Willd.?	F	Affouche	Moraceae	?	Mα
Ficus mauritiana Lam.	—	Affouche	Moraceae	R.?	Mβ
Gaertnera psychotrioides Baker	Gp	Bois banane, Bois de rivière	Rubiaceae	E.	Mβ
Geniostoma borbonicum Spreng.	Gb	—	Loganiaceae	M., R.	Mβ
Gouania tiliifolia Lam.	—	Liane charretier	Rhamnaceae	R., Rod.	Liane
Gymnochilus nudum Bl.	—	—	Orchidaceae	M.	Hc.
Haronga madagascariensis Choisy	—	Bois haronge	Hypericaceae	M., R.	Mi.
Helichrysum yuccifolium Lam.	—	Immortelle	Compositae	E.	N.
Homalium paniculatum Benth.	—	Bois de rivière	Samydaceae	R.	Mβ
Hugonia serrata Lam.	Ht	Liane à crochet	Linaceae	E.	Liane
Hugonia tomentosa Cav.	—	Liane à crochet	Linaceae	R.	Liane
Ixora parviflora Lam.?	—	—	Rubiaceae	E.	Mi.
Ixora sp.	Is	—	Rubiaceae	E.?	N.
Labourdonnaisia sp.	Lg	Bois de natte Legentil Bois de natte à petites feuilles	Sapotaceae	R.	Mα
Leea sambucina Willd.	Lc	Bois bœuf	Vitaceae	O.W.T.?	Mi.
Ludia sessiflora Lam.	Ls	Bois Mozambique	Flacourtiaceae	R., Sey., E. Afr.	Mβ
Mallotus integrifolius Muell.-Arg.	Ml	Bois pigeon	Euphorbiaceae	R.	Mβ
Memecylon angulatum Reich.	Mn	—	Melastomataceae	E.	Mi.
Memecylon cordatum Desv.	Mc	—	Melastomataceae	E.	Mi.?
Memecylon trinerve DC.	Mt	Bois canne	Melastomataceae	E.	Mβ
Mimusops maxima (Poir.) R.E.V.	Mm	Bois de natte	Sapotaceae	R.	Mα
Mimusops petiolaris Dubard?	Mi	Makak	Sapotaceae	E.	Mα
Molinaea arborea Gmel.	Ma	Bois sagaïe blanc	Sapindaceae	R.	Mβ
Molinaea cupanioides Radl.	Ms	—	Sapindaceae	E.	Mβ
Molinaea macrantha Radl.	Mo	—	Sapindaceae	E.	Mi.?
Mussaenda Landia Poir.?	M	Quinquina	Rubiaceae	E.	Mβ
Nuxia verticillata Lam.	Nv	Bois maigre	Loganiaceae	R.	Mα
Ochna mauritiana Lam.	Om	Bois bouquet banané	Ochnaceae	E.	Mi.
Ochrosia parviflora G. Don	Ob	Bois jaune	Apocynaceae	Sey., C., Mal.	Mi.

Botanical name	Ecological symbol	Vernacular name	Family	Distribution	Life form
Ocotea cupularis Cordem.	Oc	Bois canelle	Lauraceae	M., R.	$M\beta$
Olea lancea Lam.	—	Bois cerf	Oleaceae	R.	$M\beta$
Oncostemon latifolium Mez	Os	—	Myrsinaceae	R.?	Mi.
Pandanus sp.	—	Vacoas	Pandanaceae	E.	Mi.
Phajus tetragonus Reichb.	—	—	Orchidaceae	E.	Hc.
Phajus villosus Reichb.	—	—	Orchidaceae	E.	Hc.
Philippia abietina Klotzsch	—	Bruyère	Ericaceae	R.	N.
Phylica mauritiana Bojer ex Baker	—	Bruyère	Rhamnaceae	E.	N.
Phyllanthus phillyreifolius Poir.	Pp	—	Euphorbiaceae	R.	Mi.
Pilea atroviridis Baker	—	—	Urticaceae	E.	H.P.
Pilea urticifolia Bl.	—	—	Urticaceae	R., E. Afr.	H.P.
Pilea verbascifolia Wedd.	—	—	Urticaceae	E.	H.P.
Pittosporum Senacia Puttl.	—	Bois cerf odorant	Pittosporaceae	R., Rod., Sey.	Mi.
Pleurostylia leucocarpa Baker	—	—	Celastraceae	E.	Mi.
Protium obtusifolium March.	—	Bois colophane bâtard	Burseraceae	E.	$M\alpha$
Psathura borbonica Gmel.	Pb	Bois cassant à grosses feuilles	Rubiaceae	R.	N.
Psathura myrtifolia A. Rich.	Pm	Bois cassant à petites feuilles	Rubiaceae	R.	N.
Psathura terniflora A. Rich.	P_{21}	Bois cassant	Rubiaceae	E.	Mi.
Pseudannona amplexicaulis Safford	—	—	Annonaceae	E.	Mi.
Psiadia trinervia Willd.	—	Baume d'Ile Plate	Compositae	R.	Mi.
Psiloxylon mauritianum Baill.	Px	Bois Bigaignon rouge	Lythraceae	R.	$M\beta$
Pyrostria macrophylla A. Rich.?	—	—	Rubiaceae	E.?	Mi.
Quivisia oppositifolia Cav.	Q	Café marron	Meliaceae	E.?	$M\beta$
Rutidaea coriacea Baker	—	Bois de rat, Bois de canelle blanc	Rubiaceae	E.	Mi.
Sideroxylon Bojerianum DC.	—	Manglier vert	Sapotaceae	E.	$M\alpha$
Sideroxylon puberulum DC.	—	Manglier rouge	Sapotaceae	E.	$M\alpha$
Scutia Commersoni Brongn.	Sc	Liane bambara	Rhamnaceae	S.E. Asia	Liane
Securinega durissima Gmel.	Sd	Manahe	Euphorbiaceae	R., Rod.	$M\beta$
Stillingia lineata Muell.-Arg.	—	Fangame	Euphorbiaceae	R.	Mi.
Tambourissa amplifolia DC.	Ta	Bois tambour	Monimiaceae	E.	Mi.?
Tambourissa elliptica (Tul.) DC.?	Tp	Bois tambour	Monimiaceae	E.	$M\beta$
Tambourissa pedicillata Baker	T_2	Bois tambour	Monimiaceae	E.	$M\beta$
Tambourissa peltata Baker	T	Bois tambour	Monimiaceae	E.	$M\beta$
Tambourissa Sieberi DC.	Ts	Bois tambour à petites feuilles	Monimiaceae	E.	$M\alpha$
Tambourissa sp.	Tx	—	Monimiaceae	E.?	Mi.
Toddalia aculeata Pers.	To	Patte de poule à piquants	Rutaceae	S.E. Asia?	Liane
Trochetia Blackburniana Bojer	—	—	Sterculiaceae	E.	Mi.
Trochetia triflora DC.	—	—	Sterculiaceae	E.	$M\beta$
Vepris paniculata Engl.	—	Patte de poule	Rutaceae	R., Rod.	Mi.
Xylopia Richardi Boiv.	Xv	—	Annonaceae	R.?	$M\beta$
—	C	Bois Caf-Caf	Euphorbiaceae	E.?	$M\beta$

THE "MOSSES" OF THE STAINMORE DISTRICT

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(*With two Figures in the Text*)

In 1904, while mapping the vegetation of the northern Pennines, F. J. Lewis described a characteristic type of plant community dominated by *Sphagnum*. In spite of the interest of this plant community to students of moorland ecology, it does not appear that any further investigation of these areas has since been made. Hence the following more detailed account of this type of vegetation is presented. There are many features of the associated communities which would repay further study, but as, under existing conditions, it is unlikely that additional work will be practicable, this account may serve a useful purpose as well as record the main features at present existing.

The locality to be described lies on the main Pennine watershed, south of Mickel Fell and between Brough in Westmorland and Barnard Castle in Co. Durham. It lies on either side of the main road from Brough to Bowes and thence to Barnard Castle, a road which is Roman in origin and which has undoubtedly been in use since Roman times. A Roman fort and at least one camp occur on the edge of the most interesting area and this is bounded on the north by the road from Brough to Middleton in Teesdale. This area has no collective name, each ridge being named separately, but the summit ridge and western parts are called Stainmore Common. A second area south of the Brough-Bowes road is part of Stainmore Forest.

The Pennines at this point consist of a western watershed running towards the north-north-west with a series of broad ridges offset towards the east. The drainage is by a more or less parallel series of tributaries of the Tees, the Balder, Hunder and Deepdale Becks, the River Greta and Ease Gill Beck. All are mountain torrents. The general slopes are steep to the west, very gentle to the east. It is difficult to appreciate the character of the slopes from the map. To the west they are generally from 1 in 8 to 1 in 10 rising even to 1 in 5. On the east, the ruling gradients average from 1 in 35 to 1 in 80. These are often imperceptible on the ground and it is on this type of country that the especially characteristic vegetation of the area is developed.

The western escarpment generally averages about 510 m. (*c.* 1550 ft.) in height, rising to 554 m. (1689 ft.) at Black Tewthwaite and falling gradually eastwards to about 460 m. at Shacklesborough Moss. Most of the important part of the area lies between 460 and 490 m., with the tabular hills of Beldoo and Shacklesborough sticking up some 30–40 m. higher. These hills are almost the only visible reference points in a tremendous sweep of moorland, but in the northern part of the area a fence marks the county boundary (north Yorkshire and Westmorland) and south of the Balder valley scattered stones have a similar purpose. At the same time these serve as valuable fixed points and some of them are lettered on the map (Fig. 2) as the terminal points of a series of transects taken over the most interesting areas.

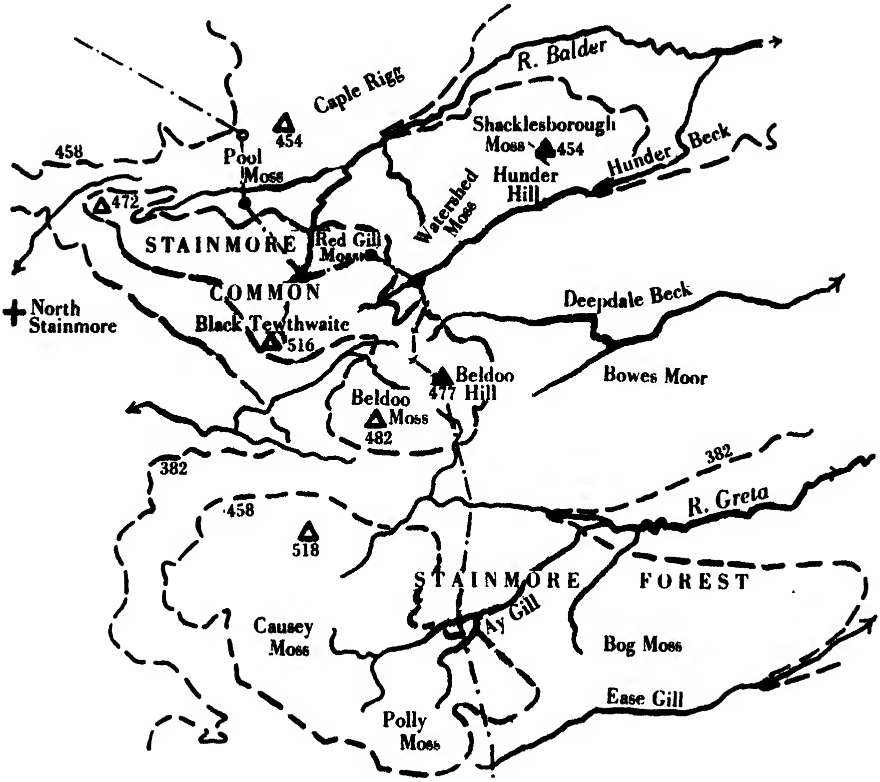

Fig. 1. The Pennines between Brough and Bowes. Altitudes in metres.

The transects carried out were:

(1) 50 m. east of the line *ABCD*, thence to *E*.
(2) From 200 m. north of *E* west (magnetic) to the escarpment.
(3) From 200 m. south of *E* to Shacklesborough Hill.
(4) From *D* to Beldoo Hill.
(5) From Hunder Hill to *F* and thence to Black Tewthwaite.
(6) Across Beldoo Moss to Beldoo Hill, thence to Shacklesborough Hill.

On these transects the vegetation of representative quadrats was recorded at intervals of 50 or 100 m. Including records from the southern area (Bog Moss, Polly Moss and Causey Moss), there are about two hundred and fifty of these records and on these the following detailed descriptions of the vegetation are based. The Caple Rigg area was also examined.

The quadrats were each 1 sq. m. in area and the records made give the species present, those abundant (covering more than one-fifth of the area) or frequent (covering more than one-twentieth of the area or more than twenty shoots). Soil samples from a depth of approximately 15 cm. were taken from chosen quadrats, carefully packed in tins. About half were treated with toluol. The pH of these was subsequently determined electrometrically and most were examined microscopically. The pH was obtained in samples treated with about three times the volume of water and saturated with quinhydrone. There appeared to be no difference between those with toluol and those untreated.

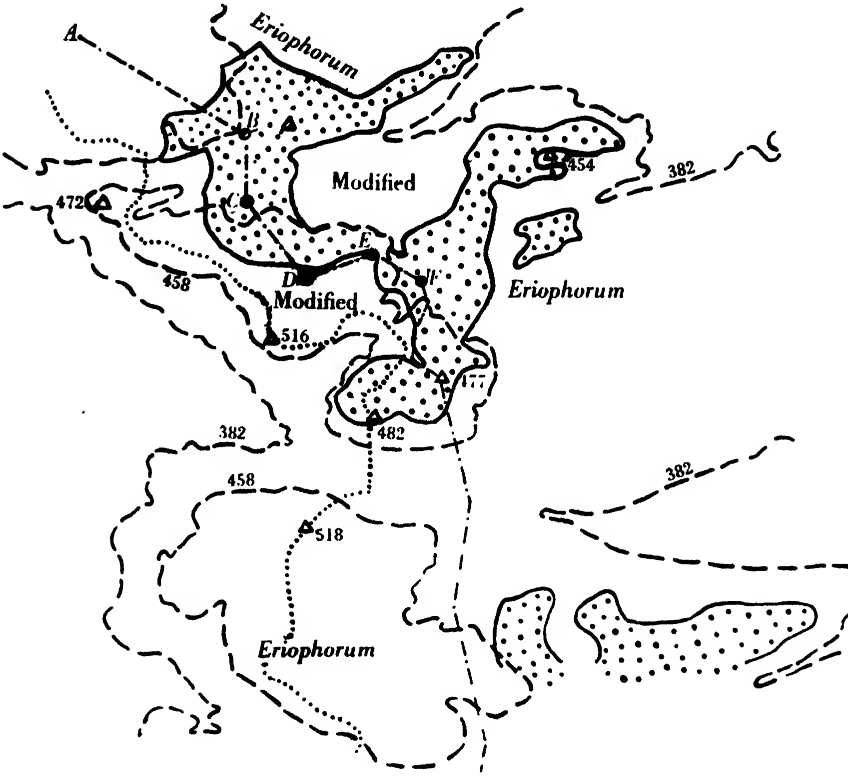

Fig. 2. Distribution of *Sphagnum*-dominated areas (shaded) after Lewis (1904). The main watershed is shown as a dotted line, the county boundary as a lettered broken line south of *A*.

Peat samples down to a depth of 4 m. were obtained on one occasion with a small Swedish peat borer by Mrs M. Bulman and Prof. W. G. Fearnsides who subsequently determined the depths of peat over a great variety of sites. My thanks are due to them for this and other help in the field and also to

Dr E. M. Lind and to Mr A. Thompson, the former for assistance in quadrat recording and the latter for determining a series of representative Sphagna.

Rainfall. The rainfall of this area is no doubt affected by the rapid upward lift given to the prevalent westerly winds by the western escarpment. Due allowance must be made for the fact that most of the area of importance lies just east of the main divide. The local topography exerts considerable influence on the cloud cover and both this and the rainfall are very much less in the main Balder valley to the east than on the adjacent ridges. Taking such features into consideration and utilizing the data available for the Lune Forest just to the north and for Upper Niddersdale to the south, the indications are that at 425–460 m. (*c.* 1400–1500 ft.) the rainfall must average about 140 cm. (55 in.) per annum and that it is unlikely to be below 125 cm. or above 147 cm.

VEGETATION: TYPES OF COMMUNITY AND THEIR INTER-RELATIONS

The *Sphagnum* community identified by Lewis covers a large part of the area as shown in Fig. 2. Lewis (1904) gave a brief general description of this community in which he stated that *Sphagnum* was dominant and that *Rubus chamaemorus*, *Erica tetralix* and *Oxycoccus quadripetala* were frequent, while *Eriophorum angustifolium*, *Empetrum nigrum* and *Calluna vulgaris* were "generally present though scarce". The boundaries of the *Sphagnum*-dominated areas given by Lewis coincide fairly well with those to-day in which *Sphagnum* is still prominent as defined below. But *Sphagnum* is evidently much less frequent in some parts, notably north and west of point *B* (Fig. 2) and in the Bog Moss area, and there may have been a considerable decrease in the *Sphagnum*-dominated area. Excepting the western escarpment, the tabular hills and the steep slopes adjacent to some of the streams, the whole of the main area is covered by peat obviously derived from a vegetation in which *Sphagnum* was very abundant.

At the present time, there are six main types of vegetation in the area. In three of these, *Sphagnum* is always present and is locally frequent to dominant. These will be called "moss", the local place-name for areas of this type. In one type, termed type A "moss", *Sphagnum* spp. are always abundant in the quadrats and the *Sphagnum* cover is continuous. In another, called type B "moss," there is no obvious damage of this cover but Sphagna are only abundant in one-half of the quadrats though always present and generally frequent. The last type of "moss" is on dissected peat and obviously a topographic derivation of type A. These three types cover most of the *Sphagnum*-dominated area of the Lewis map. Where the *Sphagnum* cover is now deficient, either *Calluna vulgaris* or *Eriophorum vaginatum* may be dominant or these species are together co-dominant. The floristic composition of these communities will be given in detail at a later stage (p. 168). It will be convenient to consider first some of their general relations.

Normally all are found on deep peat (+1 m.) except one form of the *Eriophorum* community. Over most of the area, peat is at least 3–6 m. in depth, and Lewis states that it may at times reach a depth of 40 ft. (*c.* 12 m.). There is, as might be expected, a general tendency for the deepest peat to occur on the areas of least slope, less than 1 in 60, and this is also the type of locality on which "moss" of type A is generally found. Type B "moss" occurs most often on extensive areas of distinct slope, 1 in 30 to 1 in 70, but it is also quite frequent as a fringing community on the borders of the type A "moss". Dissected "moss" occurs where the drainage systems have cut back into the peat. No areas of dissected type B "moss" are known. The *Eriophorum-Calluna* communities are commonly marginal to the main areas but not necessarily so. They are also more often on the steeper slopes and are at times found where the gradient is as much as 1 in 10, but they also extend to the gentle slopes characteristic of the "moss" types.

The character of the peat, particularly the abundance of Sphagna in it, shows that these types of vegetation have been derived from areas of the "moss" type and this confirms evidence obtained from the Lewis map. One area of particular interest lies north-west of the point marked *B* (Fig. 2). Looking north-west towards *A*, the county boundary divides land now under different treatment, all shown by Lewis to be *Sphagnum*-dominated. To the south-west of the fence, *Eriophorum vaginatum* is now dominant and, to the north-east, *Calluna vulgaris*. The whole area has been burnt, but that now *Calluna*-covered is preserved as a grouse moor, while that covered by *Eriophorum* has been much grazed. There is, therefore, direct evidence both from the peat and the Lewis map that these two communities are derived from "moss" by biotic agencies. That such changes have been widespread in the past in the areas adjacent to the existing mossland is undoubted, particularly where there is easy access as round the Hunder Beck and on the natural route from Baldersdale to North Stainmore, as well as to the south-east. Similar changes are taking place on the Bog Moss (Stainmore Forest) where extensive burning and some draining have been carried out with the object of forming grouse moor. Generally speaking increased slope evidently makes it easier to bring about these changes. The margins of the mossland are naturally attacked first, both because of the greater ease of draining and also because the sheep grazing on the narrow grassland, marginal to the streams, gradually modify the adjacent "moss" vegetation and so extend the area covered by *Eriophorum*.

A large field of work on the effects of burning on the Bog Moss (Stainmore Forest) has had to be left untouched. The first effects are commonly the destruction of the woody species and hence a swing of the balance in favour of types such as *Eriophorum*. Considerable damage is done to the *Sphagnum* cover, but it appears to suffer more from the subsequent exposure to drying and to the effects of the burning and drying on the peat. Trampling by grazing animals (here mainly sheep) seems to be particularly damaging to the surface and if this is continued the surface tends to become puddled, though increased oxidation and the effects of burning may also be partly responsible for this condition. When grazing animals are frequent, *Calluna* fails to regenerate adequately and the tussocks of cotton-grass tend to spread over the whole surface, and finally to form a closed and relatively stable community. If grazing effects are slight and possibly under other undetected conditions, the burned area passes through a stage with caespitose *Eriophorum* and bushy *Calluna* co-dominant which may, with intermittent burning and little grazing, finally become dominated by *Calluna*. This account is necessarily an outline, as much further work is required on the effects of the grazing intensity and slope as well as the season and frequency of burning as they may affect the final equilibrium reached. It is to be noted that the Lewis map shows that large areas formerly dominated by *Calluna* are now dominated by *Eriophorum*. Perhaps the clearest case of this is the area immediately north-west of Ay Gill in Stainmore Forest. This is shown on the map as Callunetum, while it is now dominated by *Eriophorum* and incidentally much grazed. As the locality has the form of a great bowl, visible from many points and part of the natural route into the hills, it is extremely unlikely that any serious error in mapping could be made. Similarly, a nearby area east of Red Gill has been converted from cotton-grass into heather moor since the date of the map. In fact, almost the whole of the mapped area on Stainmore Forest shows numerous signs of change. There is thus clear evidence that the cotton-grass and ling communities are interchangeable as well as that they are both derived from some form of the "moss" community.

DESCRIPTION OF VEGETATION TYPES

(1) *Type A "moss"*

The "mosses" usually bear vegetation of this type. The slope is often negligible and probably always less than 1 in 60. The lists given in Table 1 are from quadrat records from Red Gill Moss, Shacklesborough Moss, Bog Moss, Watershed Moss, Pool Moss, and smaller areas of Beldoo Moss and Caple Rigg, five to eight quadrats from each being included. In the field the noticeable feature is the almost continuous *Sphagnum* cover and the spongy nature of the substratum. Sphagna are abundant in all quadrats, especially *S. papillosum*, but often also *S. rubellum*. Both of these are present in 70 % of the quadrats. *S. plumulosum* and *S. cuspidatum* are more local in distribution in half the quadrats, but also at times abundant. The other Sphagna recorded are less characteristic, though *S. recurvum* is present in 25 % of the quadrats and occasionally abundant.

Of the higher plants, *Calluna vulgaris*, *Erica tetralix* and *Eriophorum vaginatum* are constantly present and *E. angustifolium* is in 90 % of the quadrats. The most distinctive phanerogams are *Narthecium ossifragum* (78 %), often abundant, and *Drosera rotundifolia* (61 %), but *Oxycoccus quadripetala* (47 %) is also noteworthy and frequent. *Andromeda polifolia* is confined to the area about Shacklesborough Moss, where it is almost constantly present. Its absence elsewhere may be a sign of modification. Of the cryptogams, *Cladonia sylvatica* (47 %), *C. floerkiana* (25 %) and *Odontochisma sphagni* (12 %) are most characteristic, mosses and liverworts being generally infrequent. The full list of species is given in Table 1.

Growth forms in this community are quite definite, *Calluna* being rarely more than 15 cm. high and not bushy. The shoots of *Eriophorum vaginatum* tend to be dispersed among the Sphagna and the plants are rarely strongly caespitose. The appearance is usually that of a low-growing sward with no clear dominant. There appears usually to be no marked microtopography. The only places where this is clearly defined are those adjacent to a dissected area and where either incipient drainage channels have formed or else a dissected area has begun to regenerate after blocking of the drainage channels. In such places there may be a regeneration complex showing a transition from depressions with *Sphagnum cuspidatum* through a *S. papillosum* sward to hummocks with *Calluna*, *Eriophorum vaginatum* and *Sphagnum rubellum*. Small pools on bare peat may occur, to be colonized by *Eriophorum angustifolium* and Sphagna, before developing in a similar manner. The vegetation of many regenerating areas tends to approximate to that of a type B "moss".

(2) *Type B "moss"*

A transect up the long slope from Baldersdale to the south and parallel to the county boundary between *C* and *D* covers a good example of a different type of community, which is also found on the rather steeper slopes surrounding or falling away from the areas of type A "moss". The slopes are still gentle, however, and range commonly from 1 in 30 to 1 in 70. The *Sphagnum* cover is much less complete, the species being abundant in only half the quadrats. *S. cuspidatum* (27 %), *S. papillosum* (50 %) and *S. plumulosum* (25 %) are noticeably less widely distributed, though *S. rubellum* (75 %) maintains a high frequency of occurrence.

The noticeable features among the phanerogams are the disappearance of *Narthecium ossifragum* and a considerable decrease in the amounts of *Drosera rotundifolia* (19 %) and *Erica tetralix* (67 %). *Empetrum nigrum* becomes very characteristic (67 %) and *Rubus chamaemorus* (17 %) is also noteworthy. With the reduction in Sphagna other bryophytes are marked, especially *Hypnum schreberi*, *Dicranum scoparium*, *Plagiothecium undulatum* and *Aulacomium palustre*, all in at least one quadrat in five. *Hylocomium loreum*, *Ptilidium ciliare*, *Calypogeia Trichomanes* and *Lophozia ventricosa* also appear to be characteristic.

Table 1. *Composition of plant communities as percentage occurrences in quadrats of one square metre*

	Type A "moss"	Type B "moss"	Dissected moss	*Calluna*	*Erio-phorum*	*Calluna = Erio-phorum*
No. of quadrats	40	40	30	25	45	25
Andromeda polifolia	15	–	7	–	–	–
Calluna vulgaris	100	97	100	100	75	100
Drosera rotundifolia	61	19	33	–	–	+
Empetrum nigrum	3	67	17	76	29	52
Erica tetralix	97	67	60	24	31	40
Galium saxatile	–	–	–	–	+	–
Oxycoccus quadripetala	47	32	13	24	4	+
Rubus chamaemorus	+	12	+	8	9	–
Vaccinium myrtillus	–	–	–	+	+	–
Carex panicea	–	–	–	–	4	–
Deschampsia flexuosa	–	–	–	–	4	–
Eriophorum angustifolium	90	75	87	28	75	40
E. vaginatum	100	100	100	96	100	100
Juncus squarrosus	–	–	–	–	55	8
Nardus stricta	–	–	–	–	4	–
Narthecium ossifragum	78	–	66	–	4	–
Sphagnum acutifolium	–	–	–	4	–	+
S. cuspidatum	45	27	20	4	31	16
S. fimbriatum	+	+	+	–	–	–
S. medium	+	–	13	4	–	+
S. papillosum	78	50	53	20	15	28
S. papillosum var. sublaeve	2	+	+	+	–	+
S. plumulosum	47	25	30	16	+	8
S. pulchrum	+	+	–	–	–	–
S. recurvum	21	17	10	–	+	–
S. rubellum	70	75	50	52	22	68
S. tenellum	5	+	7	4	–	8
Aulacomium palustre	+	20	+	20	22	20
Campylopus flexuosus	–	+	7	–	13	+
Dicranum scoparium	7	22	10	32	16	16
Hylocomium loreum	–	10	–	8	–	12
Hypnum cupressiforme	12	+	43	32	–	20
H. fluitans	+	+	–	–	4	–
H. schreberi	10	20	10	36	–	16
Plagiothecium undulatum	5	27	7	60	7	28
Polytrichum commune	–	–	–	–	13	+
Rhacomitrium lanuginosum	+	–	7	4	–	–
Webera nutans	–	–	–	+	+	+
Calypogeia trichomanes	5	12	10	20	22	20
Diplophyllum albicans	5	+	–	8	20	+
Gymnocolea inflata	7	–	7	–	11	–
Leptoscyphus taylori	+	–	+	–	–	–
Lophocolea sp.	–	–	–	–	+	–
Lophozia ventricosa	+	7	+	4	24	–
Odontochisma sphagni	12	+	+	–	–	–
Ptilidium ciliare	–	7	–	12	51	20
Tetraplodon mniodes	–	–	+	–	–	–
Cladonia coccifera	+	–	7	8	–	+
C. floerkiana	25	5	27	12	–	12
C. sylvatica	47	42	80	28	4	40
C. uncialis	+	+	10	–	–	–
Parmelia physodes	–	+	+	4	+	8
Zygogonium ericetorum	–	+	+	–	–	–

The growth forms of the individual plants are less regular than in type A "moss" and the vegetation looks much more ragged. It is not impossible that these areas of gentle slope have, in the past, suffered some modification either at the hands of shepherds and gamekeepers or as a result of the more definite modification of adjacent areas. It seems advisable for the present, however, to regard them as a variation of type A "moss" under less stagnant conditions, especially as these types of vegetation are often continuous, type B receiving the drainage from type A. It seems reasonably certain that peat accumulation is still taking place in the type B areas, perhaps mainly in the winter months in more typical years but even in summer during wet years.

(3) *Dissected "moss"*

This type of "moss" is found where peat dissection has occurred through the development of natural drainage channels in the peat. So far as can be told there has been no burning and little grazing. The natural vegetation cover of the peat has therefore persisted unchanged and in particular the cryptogam cover has developed little damaged. The quadrats given are from places within 5–30 m. of a drainage channel. Extremely dissected places are not included, but it should be noted that the vegetation there is essentially similar. Dissected moss occurs on and around Beldoo Moss and Shacklesborough Moss and also along the drainage streams descending from Black Tewthwaite. Much of the area marked as Callunetum on the Lewis map is of this type.

It may be convenient to conclude this section by giving lists of the characteristic species of each type:

"Moss" A. *Erica tetralix*, *Narthecium ossifragum*, *Drosera rotundifolia*, *Sphagnum cuspidatum*, *Odontochisma sphagni*, locally *Andromeda polifolia*.

"Moss" B. *Empetrum nigrum*, *Sphagnum rubellum*, *Rubus chamaemorus*, *Plagiothecium undulatum*, *Aulacomium palustre*, *Lophozia ventricosa*, *Ptilidium ciliare*, *Hylocomium loreum*.

Dissected moss. *Sphagnum medium*, *Cladonia sylvatica*, *C. coccifera*, *Hypnum cupressiforme*, *Campylopus flexuosus*, *Rhacomitrium lanuginosum*.

Modified areas. The areas in which modification of the original "moss" vegetation has taken place tend to be marginal but normally show clear signs of burning, grazing or draining. The slopes at the heads of the Hunder Beck and Balder valleys are of most interest, though large areas to the north and east appear to belong to the same types, dominated by *Calluna*, or *Eriophorum vaginatum*, or with these species co-dominant. The inter-relations of the communities have already been indicated.

(4) Calluna *dominant*

In addition to a general comparative list given in Table 1, records from three examples of this community are given in Table 2. The first, *Ca* 1, is from a transect of about 400 m. parallel to the upper reaches of the Hunder Beck from the county boundary at *F*. It appears to have been burnt at some time in the past and is partly drained by a series of infrequent natural gutters in the peat, as well as by a few shallow artificial drains of recent origin. The second group of records, *Ca* 2, is from north-east of the county boundary at *B*. This has been burnt and modified since the Lewis map of 1904, and is maintained as grouse moor. The third series, *Ca* 3, is from the slopes to the north of Beldoo Hill and Moss, mainly on dissected peat with many signs of burning. The examples all appear to lie on deep peat. While these areas show certain differences, they are alike in having *Eriophorum vaginatum* constantly present though usually inconspicuous. *Empetrum nigrum* (76 %) is the characteristic associate, though *Oxycoccus* also maintains itself. Sphagna are present in small amounts in most quadrats though frequent only in one quadrat in five. Shade forms of *Sphagnum rubellum* are most usual. The more frequent mosses are *Hypnum cupressiforme* (32 %), *H. schreberi* (36 %), *Dicranum scoparium* (32 %) and *Plagiothecium undulatum* (60 %). *Aulacomium palustre* (20 %) and *Calypogeia trichomanes* (20 %) are sparse but fairly widespread. The three species of *Cladonia*, *C. sylvatica* (28 %), *C. floerkiana* (12 %) and *C. coccifera* (8 %), are confined mainly to dissected areas. *Plagiothecium* and *Aulacomium* are found mostly in zones 1 and 2, which may have been derived from type B "moss".

Small areas on Beldoo Hill and Black Tewthwaite may possibly represent a natural Callunetum but these possess closely similar species and are also subject to burning.

(5) Eriophorum vaginatum *dominant*

Communities of this type appear to fall into three groups. In the first of these, *E* 1 in Table 2, the peat is deep, well over 1 m., and probably usually from 3 to 5 m. in depth. Characteristic areas of this type lie south-west of the county boundary at *B* and also along the north side of the Hunder valley below *F*. These have been modified from moss according to the Lewis map. The latter example has a series of shallow parallel drains in it. Because these communities appear to be still undergoing change and because of the considerable exposure of bare peat, it is probable that the vegetation is still unstable. Both show many signs of grazing, sheep tracks, droppings and trampling of bryophytes. The second type of community (*E* 2) is also on deep peat but differs floristically. The cotton-grass now almost completely covers and shades the surface. This type is very extensive south of the main area and west of the Bog Moss. The records are from Polly Moss and Causey Moss; both areas are known to have been in the same condition for the last fifteen years. This type is regarded as a stable development of *E* 1. The underlying peat is of the type general below "moss" though much darker in colour. The third type of community, *E* 3, occurs on shallow peat averaging about 35 cm. in depth (range 20–45). This is frequent about Hunder Hill but is quite widely distributed. The peat, though much oxidized and amorphous, still contains numerous remains of Sphagna and was presumably formed by something like type B "moss". The community is fairly characteristic of the slopes adjoining

Table 2. *Detailed composition of* Eriophorum *and* Calluna *communities*

Community ...	*Eriophorum*			*Calluna*		
Type ...	*E* 1	*E* 2	*E* 3	*Ca* 1	*Ca* 2	*Ca* 3
No. of quadrats ...	15	15	15	11	8	6
Calluna vulgaris	9	14	11	11	8	6
Empetrum nigrum	5	6	2	10	6	3
Erica tetralix	5	8	1	—	2	4
Galium saxatile	--	—	1	—		—
Oxycoccus quadripetala	2	—	—	4	1	1
Rubus chamaemorus	3	1	--	1	1	
Vaccinium Myrtillus	—	-	1	—	1	—
Carex canescens	-	1	—	—		
C. panicea	—	-	1	—	—	—
Deschampsia flexuosa	—	—	2	--	—	—
Eriophorum angustifolium	10	11	13	3	2	2
E. vaginatum	15	15	15	11	7	6
Juncus squarrosus	8	5	12	—		-
Nardus stricta	-	—	2	—		
Narthecium ossifragum		2		—	—	
Sphagnum acutifolium	—		--	1	-	—
S. cuspidatum	9	1	4	—		1
S. medium	—	-	—	1	--	—
S. papillosum	3	4	--	3	--	2
S. plumulosum	3	1		2	1	1
S. recurvum		—	1	—	—	--
S. rubellum	8	2		7	4	2
S. tenellum	—		—	-	1	—
Aulacomium palustre	7	2	1	3	2	-
Campylopus flexuosus	2	2	2	—	-	
Dicranum scoparium	5	-	2	3	3	2
Hylocomium loreum	--	-	—	—	2	-
Hypnum cupressiforme		—	--	3	1	4
H. fluitans	—	-	2	—	—	—
H. schrebori	—			4	3	2
Plagiothecium undulatum	2		1	8	6	1
Polytrichum commune	1	2	3	—		-
Rhacomitrium lanuginosum	--	—	—	--		1
Webera nutans	—	-	1	1	—	—
Calypogeia trichomanes	3	1	6	4	1	--
Diplophyllum albicans	2	7		2		
Gymnocolea inflata	1	3	1	—		
Lophocolea sp.	—	—	1		—	—
Lophozia ventricosa	4	2	5	—	1	-
Ptilidium ciliare	7	12	4	3	—	-
Cladonia coccifera	2	-	—	—	1	1
C. floerkiana	-				1	2
C. sylvatica	—				1	6
Parmelia physodes	—	-	1	—	—	1

strips of pasture along the upper watercourses, but also caps several of the slight ridges.

Eriophorum vaginatum is always strongly caespitose and the ericacious species usually grow on the tufts. The heavy shade on the peat probably limits the development of the Sphagna and other mosses. Of the more widely spread species shown in Table 2, some like *Empetrum*, *Eriophorum angustifolium* and *Lophozia ventricosa* are generally distributed, but many of the others are more or less local. Thus *Calluna* though always sparse is most general in the stable areas like *E* 2, and least so in the unstable. *Erica tetralix* appears to prefer deep peat. *Juncus squarrosus* is particularly frequent on the shallow peat. Of the bryophytes, Sphagna are usually present only as scraps (58 % of the quadrats) and are never more than frequent. *Sphagnum cuspidatum* is most typical and with *S. rubellum* is most frequently found in the unstable type of community, *E* 1, with *Aulacomium palustre. Calypogeia trichomanes* is most often on shallow peat. *Diplophyllum albicans*, perhaps *Gymnocolea inflata*, and especially *Ptilidium ciliare* are characteristic of the stable form of the community.

In contrast with the *Calluna* community already described the greater number of liverworts is striking as also is the decrease in ericaceous species. Another point of interest is that *Eriophorum* is dominant on steeper as well as on similar slopes to those dominated by *Calluna.* If there is some seepage from above, they may be as steep as 1 in 8.

(6) Calluna *and* Eriophorum vaginatum *co-dominant*

This community is clearly intermediate between the two last described (see Table 1). *Calluna* is usually tall and the cotton-grass strongly caespitose so that the peat surface is shaded. Floristically, also, it bears obvious resemblances to the type B "moss", differing mainly in the incompleteness of the *Sphagnum* cover. Sphagna are present in about 70 % of the quadrats but are rarely even frequent. The community seems to arise from any of the "moss" types as a fairly stable stage after burning. Most commonly it is on moderate slopes (*c.* 1 in 20 and 1 in 30) and there is generally some grazing. It may perhaps be assumed that the decrease of some species is the result of burning. In this category may come *Eriophorum angustifolium*, *Erica tetralix*, *Oxycoccus*, *Rubus chamaemorus* and *Narthecium* as well as the more characteristic Sphagna. *Empetrum nigrum* is the most characteristic associate.

In one form or another, this community is common in the northern Pennines. In a previous paper (Pearsall, 1938) examples of it were termed "mixed moor".

SOIL CONDITIONS

The only set of soil conditions investigated in any detail is the hydrogen-ion concentration. For this two sets of samples were collected, one in April and the other in September. The data are summarized in Table 3. From this it is apparent that the "moss" peat of type A has usually a *p*H value between 3·8 and 4·0. Where oxidation takes place, as on the "dissected moss" peats, the values fall to between 3·45 and 3·6, while a similar if smaller fall to *p*H 3·5–3·7 occurs on the peats of type B "moss", implying that there also oxidation has taken place. Both the latter habitats with a different flora have a similar *p*H range. The *Calluna* peats sampled tend to be more acid, *p*H 3·35–3·53, probably implying a still greater degree of oxidation. However, burning alone is associated with a fall in *p*H (Pearsall & Lind, 1941). Thus an area of slightly modified "moss" which had been partly burned the previous year gave *p*H values of 3·61 and 3·59 where burned and 3·86 and 3·81 where unburned on closely adjacent sites. It is not possible to say whether the fall is due solely to the exposure and partial oxidation of the surface peat, but it is characteristic of all recently modified areas and the facts may suggest the possibility that the type B peats are not altogether free from similar effects.

Table 3. *Peat* pH *values for different communities*

Community	April	September
"Moss" A	3·92, 3·92, 3·90, 3·89, 3·87, 3·72	4·01, 3·86, 3·84, 3·78
"Moss" B	3·69, 3·51	3·74, 3·61, 3·60
Dissected "moss"	3·69, 3·59, 3·50, 3·45	3·63, 3·61, 3·59, 3·51
Calluna	3·47, 3·35	3·53, 3·42
Calluna = *Eriophorum*	3·71, 3·60, 3·45	3 55
Eriophorum:		
Deep peat*	3·68, 3·65	3·51, 3·60
Stable, *E* 2		3·83, 3·80
Unstable *E* 1	3·40	3·38, 3·31
Shallow peat	3·73, 3·64, 3·44	3·84, 3·63

* Not otherwise classified.

The peats under *Eriophorum* show the widest range of *p*H. If the records are divided into the types already distinguished, it appears that the recent and unstable types tend to have a low *p*H, 3·3–3·4, while well-established types appear to have a higher *p*H, reaching values at Polly Moss and Causey Moss of 3·80 and 3·83. The shallow peats cover almost the whole range and areas with *Calluna* co-dominant fall within this range. If any conclusion is to be based on these figures, it must be that while the origin of the Eriophoretum may be associated with edaphic changes (leading to lower *p*H), the community may become stable under soil conditions not obviously different (as far as *p*H is concerned) from any of the other communities. If we conclude that soil conditions, as shown by *p*H are not associated with the maintenance of the cotton-grass community, then we must conclude that it is mainly biotic in origin, a conclusion which agrees with field observation.

One other feature of interest in regard to peat *p*H values is the change of *p*H with increasing depth. A series of samples was obtained from different depths (with a small Swedish peat borer), in an area of "moss" with a few dissections in the vicinity, so that the surface *p*H was low. The results were:

Depth in m.	0	1	2	3	4
*p*H values	3·61	3·87	4·26	4·41	4·68

The figures presumably show the effects of increasing oxidation at the surface. All the samples below 10 cm. were waterlogged and this is certainly their normal state. In organic soils which have always been waterlogged, *p*H values below 5·2 are unusual. Either, then, acids formed at the surface have gradually diffused downwards through the whole depth of peat, or else the lower peats must have been oxidized at some earlier time in their history and have retained the effects in part in spite of long-continued submergence.

The peats of type A moss are very wet and are quite waterlogged throughout the six winter months. They are certainly generally waterlogged below 5–10 cm. even in the drier periods in summer. The type B peats are more often in this condition but are certainly waterlogged for long periods. The former types have reducing properties at 10 cm. in summer; all others are feebly oxidizing in the surface layers.

GENERAL CONSIDERATIONS

The general problems presented by these plant communities are of some interest. The impression gained from the examination of the whole area is that it was formerly covered wholly by the "moss" type of vegetation or near derivatives. Reliable evidence of this would no doubt follow from a more detailed examination of the peat. Near the surface this always seems to consist mainly of *Sphagnum* with remains of Eriophora and Ericaceae fairly frequent or locally abundant, suggesting an originating community very similar in composition to that now dominant in the "moss" types. In the lower peats, a commonly observed type of stratification shows from 1 to 3 m. of light-coloured, rather open *Sphagnum* peat, overlying a dark-coloured partly oxidized peat in which *Eriophorum* remains are much more noticeable (though *Sphagnum* is still abundant), generally 1–2 m. in depth. Below this there is a closer, more amorphous peat, often, and perhaps generally, containing wood remains. Lewis, however, states that no wood occurs under the *Sphagnum* community, though elsewhere it is found up to 640–700 m.

These observations would suggest that the woodland community originally covered most of the slopes but perhaps not the more nearly flat plateaux. It was followed by a peat-forming "moss" community of some type and at some subsequent stage the peat was oxidized and consolidated, the *Sphagnum* remains being much compressed. A final active stage of "moss" growth followed, which has persisted until the present, though the peats examined suggest that the proportion of *Sphagnum* may have decreased as this period developed. In the areas under type B "moss" and the derived types of vegetation, the surface peat is always much more oxidized and darker than under type A "moss", and acquires a superficial resemblance to the lower strata of the normal peat succession. It is possible that the lower strata may have been formed by a community akin to type B "moss" and that this may have developed into the A type later. The present extent of the type B may lend some support to this suggestion and may be due either to slight biotic modification of the A type or to a general climatic change. If the latter were the case it might strengthen the possibility that type B is an up-grade community though there is little direct evidence of this. The available evidence suggests that most of the plant communities described came from moss of type A excepting perhaps the Eriophoretum on shallow peat.

In regard to this, a curious point arises from the peat borings (mostly carried out by Prof. W. G. Fearnsides and Mrs M. Bulman), which showed that the peat depths were all either well over a metre or else below 45 cm. This may suggest that the shallow peats came from redistributed moss peat or, if developed *in situ*, were so much oxidized as to be considerably reduced in volume. The latter would, of course, be the case if they were redistributed. No clear evidence of the mode of origin of these shallow peats was obtained however though the samples examined contained many highly oxidized remains of Sphagna though largely amorphous. It is, moreover, inherently probable that even when the moss vegetation was at its maximum extent some topographic modification existed on the ridges and steeper slopes. This may have been the type B moss or some other community in which Sphagna were prominent.

Lastly, it may be worth noting that any increase in climatic humidity would almost certainly lead to a great extension of the moss types of vegetation in the area. The general impression gained is that they would extend again to cover a much wider area if the existing biotic agencies were removed. As conditions are, it may be only a matter of years before these distinctive types disappear. There seems to be no evidence in this area as to whether the *Calluna* and *Eriophorum* communities would be stable if the existing biotic influences were not operating, but the evidence seems clear that they are biotic in origin.

SUMMARY

1. The *Sphagnum* "mosses" in the northern Pennines, recognized by Lewis, are described.

2. They occur on gentle slopes, less than 1 in 30, in an annual rainfall averaging approximately 140 cm. (55 in.).

3. Modification of these "moss" communities, due mainly to burning and grazing, apparently leads to the production of communities dominated by *Calluna vulgaris* and *Eriophorum vaginatum*.

4. The soil pH of the typical *Sphagnum* "moss" is typically between 3·8 and 4·0 but may fall to 3·45 in areas subject to modification and subsequent oxidation.

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REVIEW

THE JOURNAL OF ANIMAL ECOLOGY

VOL. 9, NO. 2, NOVEMBER 1940

THIS number contains ten original papers, eight reviews and 112 "Notices of Publications on the Animal Ecology of the British Isles". An important study by O. W. Richards, of the biology of the small white butterfly (*Pieris rapae*) and factors controlling its numbers, contains a mass of quantitative material about density, parasites, and food habits, climatic influences, etc. The author is able to account for about 75% of the mortality of each generation by known factors. K. Mellanby describes experiments done on five species of insects in North Finland in order to determine their activity under cold conditions. Two papers deal with gall midges. H. F. Barnes continues his account of changes in the populations of the button top midge (*Rhabdophaga heterobia*) on *Salix triandra*, and finds that although the fluctuations in both species tend to be parallel, parasitic infestation of the host up to high levels apparently does not control the numbers. D. P. Jones deals with the cycles of oviposition on grasses of the wheat blossom midges *Contarinia tritici* and *Sitodiplosis mosellana*, and factors affecting them. Most of the observations refer to *Alopecurus pratensis*. Two papers deal with the food of fish—G. H. Swynnerton and E. B. Worthington with four species in Haweswater, and Isobel Radforth with four species from rivers in England and Scotland. These analyses throw a good deal of light on the feeding habitats of the different fish, as well as on their food preferences. Another study of freshwater communities is by J. R. Erichsen Jones, on the effects of lead pollution upon the recovery of fauna in the river Melindwr in Wales, done by means of a detailed quantitative sampling at stations along a transect down the river. Dennis Chitty continues his account of fluctuations in Arctic animals, in the Canadian Arctic Wild Life Enquiry for 1938-39, which describes from the reports of field observers the period of decline in predators dependent on the lemming, in a good many parts of the region studied. Another Arctic contribution, by M. J. Dunbar, deals with four key species of animals in the plankton of a fjord in West Greenland, about Lat. 70° N. By measurement of the sizes and breeding condition of the Chaetopod *Sagitta elegens arctica*, and the three Crustacea *Thysanoessa inermis*, *T. raschii* and *Boreomysis nobilis*, he obtained evidence about their breeding cycles and minimum lengths of life. Two papers deal with intertidal communities. L. C. Beadle and J. B. Cragg studied the intertidal zone of two freshwater streams in the Inner Hebrides, and established the limits of a number of species in terms of tide-level and stream gradient. They also add to the curious problem of habitat distribution in the species of *Gammarus*. The paper by H. B. Moore and N. G. Sproston is a continuation of an ecological succession survey by Moore on a rocky shore at Plymouth. Full details of both plants and animals are given, the community having developed quickly towards a climax after about four years, and the numbers of plant species being 14, of animal species 71.

Reviews cover the August number of the *Journal of Ecology*, the International Wildfowl Enquiry's monograph on wild geese and duck in Scotland, the intertidal surveys of Capetown University along the coasts of Africa, the plankton transects organized by Hull University in the North Sea, adaptive coloration in animals, the *Victoria County History* zoology volumes for Oxfordshire and Cambridgeshire, the scientific results of the British Trust for Ornithology, soil conservation, and the behaviour of moorhens.

CHARLES ELTON.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING, 1940

A MEETING of the Society was held at 10 a.m. on Saturday, 6 April, in the rooms of the Linnaean Society, Burlington House, Piccadilly, London, the President, Mr C. Diver, being in the chair, and fifty to sixty members present. Mr J. D. U. Ward was elected a member of the Society. The morning was taken up by a discussion on "The factors which differentiate marsh, fen, bog and heath", and the following papers were read:

H. GODWIN:	Introduction to the discussion.
M. BULMAN:	Water relations of raised-bog and blanket-bog.
W. H. PEARSALL:	Characteristic features of bog, moor and heath.
E. M. LIND:	Connemara bogs.
P. W. RICHARDS:	Bryophyta of marsh, fen, bog and heath.

There followed a very lively discussion, from which were apparent very great deficiencies in our knowledge of these communities and habitats.

In the afternoon Dr O. W. Richards took the chair and the meeting was concluded with two most interesting papers on habitat selection:

T. T. MACAN:	Habitat selection in Corixid bugs.
D. LACK:	Habitat selection in Heathland birds.

The meeting closed with a hearty vote of thanks to the Council of the Linnaean Society for their kindness in having provided accommodation for the meeting under difficult war-time conditions.

ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, CAMBRIDGE

7–8 JANUARY 1941

Soirée in Clare College, Cambridge

ON the evening of Tuesday, 7 January, about sixty members and guests attended a soirée in the Combination Room of Clare College. During the course of it Mr Frank Kendon of St John's College showed a very beautiful series of coloured lantern-slides, photographs taken on Agfa colour film with a Leica camera. They included very faithful portraits of many plants of particular interest, the oxslip, primrose, cowslip and hybrids, *Crataegus oxyacanthoides* and *C. monogyna*, and fully demonstrated the great potentialities of colour-photography for ecological recording. Before the gathering broke up hearty thanks were offered to Mr Kendon, and to the Master and Fellows of the College, for having so kindly allowed the use of the Combination Room.

The Annual Meeting

The twenty-seventh annual meeting of the Society was held next morning, at 10 a.m., in the Botany School, Cambridge, the Vice-President, Dr A. S. Watt, in the chair and between twenty-five and thirty members present.

Apologies for absence were read from the following Council members, the President, Dr O. W. Richards, Mr Elton, Prof. Pearsall and Prof. Salisbury.

The minutes were read of the last Annual Meeting at Oxford and of the Easter Meeting in London: both were confirmed and signed.

Mr Summerhayes then gave a provisional statement on the financial position of the Society, and reported an approximate surplus of £100 on the year's working. Reductions in production costs by the editors of both journals had offset a definite diminution in subscriptions. The Hon. Editors were thanked for their industry and care, and Dr Godwin pointed out that as the finances for the past year had been determined by the conditions of *early* 1940, considerable reduction of income must still be expected and no opportunity should be missed of securing new members or retaining old ones. The meeting agreed to accept the recommendation of the Council to make a grant of £10 to the Fresh Water Biological Association in 1941. A hearty vote of thanks was given by the meeting to the Hon. Treasurers for their arduous and effective services, and in replying Dr Watt appealed once more for members to pay subscriptions by Banker's Orders. The permission granted by Council to the Hon. Treasurers to obtain new auditors, if the old were not available, was endorsed.

The report of the Hon. Secretaries on the work of the Society in 1940 was approved in the form passed by the Council.

Hon. Secretaries' Report for the year 1940

The twenty-sixth Annual Meeting of the Society was held in the Department of Botany of the University of Oxford on Wednesday, 3 January. On the previous evening a soirée had been given in the Department to about sixty members and guests, and a long and interesting series of exhibits had been displayed, illustrating plant and animal ecology being done in Oxford. The Annual Meeting was held on the Wednesday morning and after business had been completed the meeting proceeded to a series of very interesting short papers, which was continued through the afternoon. In the afternoon the Society discussed the "Application of Ecology to Present Economic Problems" and carried a motion urging more active utilization of the services of biological research workers. It was also agreed that the Society should put in hand the publication of some material for the Biological Flora. On the following morning, 4 January, the meeting was resumed with further short ecological papers. The Society is much indebted to Prof. and Mrs Osborn and Dr Clapham for their kindness and trouble in arranging a most successful meeting.

A one-day meeting of the Society was held on Saturday, 6 April, in the rooms of the Linnaean Society, London, on the Factors which differentiate Marsh, Fen, Bog and Heath, and later on the Factors determining Habitat Selection by Animals. Both proved very stimulating. The Society much appreciated the courtesy of the Council of the Linnaean Society in providing such convenient facilities during war time.

Preliminary arrangements for holding a Summer Meeting at Exeter were cancelled by the Council in view of the unfavourable development of the war-time situation.

In the past year two numbers of vol. **9** of the *Journal of Animal Ecology* have been issued, appearing in May and November and containing respectively 180 and 176 pages. Twenty original papers, with one plate, in addition to reviews, the Society's notices and the notices of publications on Animal Ecology were issued in them.

Two numbers of the *Journal of Ecology* have been issued since the last Annual Meeting:

they appeared in February and August and contained respectively 257 and 239 pages. Twenty-three original papers were published with 28 plates, as well as notices, reviews, summaries of literature and the obituary of Prof. H. C. Cowles. There has been a deliberate contraction of the size of both journals to meet the need for economy, but this has had no effect on their quality.

Following the removal of Mr Marsden-Jones from Potterne the Society's Transplant Experiments have had, regrettably, to be brought to a close. We await with considerable interest the publication by Mr Marsden-Jones and Dr Turrill of final reports on the results of these experiments.

The help of the Society has been enlisted by three groups of biological research workers engaged in work of national importance, and British members have been circulated for information in regard to *Euonymus europaeus*, the Annual Sunflower and various drug-yielding plants.

During the year the membership of the Society has fallen from 361 to 335 members, 38 members having died or resigned and 11 new members having been elected. Of the present membership list 177 members receive the *Journal of Ecology* alone, 108 the *Journal of Animal Ecology* alone, 48 both journals and 2 neither.

The Society records with regret the loss by death of two of its most distinguished members, Prof. H. C. Cowles, who was an Honorary life member, and Dr J. Burtt Davy, who inspired so many of our Colonial Foresters with an interest in ecology. The Council hopes that it will continue to receive the active support of all its members and it proposes to continue the journals and meetings of the Society as normally as circumstances allow.

The two Secretaries were thanked by the meeting for their energetic and successful handling of the affairs of the Society. It was agreed to leave to the Council the arrangements for future meetings: it was decided that a summer meeting should be held if possible. Prof. Osborn and Dr Butcher suggested the suitability of Oxford and of Nottingham for such a meeting.

Officers of the Society were then elected as follows:

Hon. Editor of the Journal of Ecology: Prof. W. H. PEARSALL.
Hon. Editor of the Journal of Animal Ecology: Mr C. S. ELTON.
Hon. Secretaries: Dr H. GODWIN and Dr G. C. VARLEY.
Ordinary Members of Council: Dr T. T. MACAN, Dr G. E. BLACKMAN, Mr A. FOGGIE, Dr A. L. HARVEY.
[*Retiring Council Members:* Prof. E. S. RUSSELL, Mr D. LACK, Mr F. T. K. PENTELOW.]

The ordinary members of the Council were elected by ballot from names put forward by the Council.

The following report was then read, and after discussion was approved.

Action taken towards a Biological Flora. At a Council Meeting held in February, Dr Clapham produced an outline scheme, and after discussion Dr Clapham, Dr P. W. Richards and Prof. Pearsall were empowered to prepare an outline of accounts of selected species of Juncus. A questionnaire has been circulated, and although no replies have been received, the accounts will be prepared.

A further report was then read:

Action taken on utilization of services of biologists during war time. Following the resolution passed at the Annual Meeting at Oxford in 1940 the Council discussed the matter at a meeting on Monday, 5 February, and a small Committee consisting of the President, Dr Godwin, Dr O. W. Richards, Dr Clapham and Dr Jones were asked to deal with the matter. An inquiry form was drawn up and circulated to members of the Society, and a large number of lengthy and valuable replies was received. These were analysed and an extensive summary was made, quoting concrete instances of the possibilities which had been suggested. Use was made of this memorandum to put the views of the Society before suitable influential biologists. The two Hon. Secretaries discussed it with the Secretary of the Agricultural Research Council, and copies were sent to all the members of the special panel for zoology and botany of the Central Register. Copies were also sent to the Society of Experimental Biologists and the Association of Applied Biologists. The former body has now taken action; and Dr Godwin, Dr Richards and Dr Clapham attended an informal meeting with representatives of the latter Society, the strong recommendation of this meeting being forwarded to the special panel of the Central Register. It is possible that the considerable recent expansion in the research staffs of the Ministry of Agriculture and Fisheries has been assisted by our activities.

The Committee has not thought it wise to call public attention to the matter through the Press since the war situation made the time very unfavourable for this. The matter has been allowed to rest at this stage.

An active discussion followed, in which Dr G. E. Blackman, Mr Middleton, Mr Summerhayes and Prof. Osborn took part, and it was agreed that the Committee should co-opt Dr Blackman and continue its work by keeping contact with other Societies, particularly in their attempts to work through the Hankey Committee, and the Institution of Professional Civil Servants.

The business meeting ended at 11.25 a.m.

Dr P. W. Richards described very interesting results of recent observations on the soils of lowland tropical regions, and their vegetation. He made a very strong case for the recognition that following differences in parent rock, tropical red-earths and well-developed podsols develop side by side in the same climate, the podsols chiefly upon coarse sandstones poor in clay and bases from the outset. This phenomenon was present both in South America and in Malay, and in both regions the two soil types bore distinct climax vegetation types. The importance of these results for the polyclimax theory of vegetation was recognized in the discussion in which the Vice-President, Mr Blackman, Prof. Tansley, Dr Rayner and Prof. Osborn took part.

Miss M. F. Mare followed with an account of food relationships in a marine bottom deposit. The macrofauna of the Rame Mud off Plymouth is composed largely of "detritus feeders" such as *Cucumaria*, which swallow mud. By putting successive dilutions of mud into suitable culture media approximate figures were obtained for the population densities of the members of the microfauna and flora of the mud from bacteria upwards. From the average size of each species the volume of living protoplasm per c.c. of mud was estimated, and found to be very small compared with the volume of the fallen planktonic organisms, which appear therefore to provide the chief food of the macrofauna. Dr Varley and Prof. Tansley asked questions at the end of the paper.

The meeting was continued in the afternoon, when Dr E. W. Jones read a paper on "Soil hardness as a factor influencing Woodland Vegetation". He showed lists and instanced experiences which suggested that soil hardening caused by grazing, coppicing or other means, may greatly affect the floristic composition of woodland undergrowth. Plants sensitive to hard soil include (1) fibrous-rooted species such as *Rubus*; (2) rhizomatous species such as *Mercurialis* and *Circaea*; (3) geophytes such as *Scilla* and *Ranunculus ficaria*. Dr Jones showed photographs illustrating the early effects of compacting upon selected metre quadrats in different woodland soils. Striking results were apparent, but the discussion tended to stress the admitted complexity of the experimental treatment. Dr Watt, Mr Blackman, Dr Godwin, Dr Richards and Mr Elflyn Hughes spoke in the discussion.

Dr H. Godwin then followed with a description of Peat profils and Pollen analyses from the Somerset Levels. He compared the Levels with the East Anglian Fenland and noted the distribution of derelict raised bogs, which still however showed a clear-cut division between an old, dark lower *Sphagnum-Calluna* peat and an upper unhumified *Sphagnum* peat. The boundary between the two was related to several archaeological horizons and to the pollen-analysis sequences at selected sites. The boundary horizon was shown to correspond with a considerable change in forest composition which could be paralleled by similar change elsewhere in Britain: this was illustrated by sequences from Shropshire and Barton Broad, Norfolk. Dr Watt, Dr Clapham, Mr Blackman, Mrs Bulman and Prof. Tansley took part in a discussion chiefly concerning the relation of this evidence to relative movement of land and sea level.

At the close of the meeting Dr Watt expressed the deep gratitude of the Society to Prof. Brooks, who had given the hospitality of his department and had kindly provided refreshments at the soirée, and to the Hon. Secretaries for the arrangements they had made.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1940

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and *less* Payments in advance:						
Members taking *Journal of Ecology* only	199	17	10			
Members taking *Journal of Animal Ecology* only	132	10	0			
Members taking both Journals	101	4	9			
Associates		15	0	134	7	7
Interest on Investments	46	15	0			
Interest on Deposit Account		8	10	47	3	10
Index volume to *Journal of Ecology*, vols. I–XX:						
Sales	9	0	0			
Expenses	3	17	10	5	2	2
				£486	13	7
Journal of Ecology, 1940:						
Sales: Current vol. **28**, 1940	497	13	6			
Back volumes and parts	50	18	3			
Reprints of papers	69	18	0	618	9	9
Advertisement					10	0
				618	19	9
Balance (see above, under Expenditure)				141	16	2
				£760	15	11
Journal of Animal Ecology, 1940:						
Sales: Current vol. **9**, 1940	231	16	2			
Back volumes and parts	15	4	8			
Reprints of papers	49	9	6	296	10	4
Balance (see above, under Expenditure)				186	7	6
				£482	17	10

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing and Stationery	7	3	9			
Postages	8	6	4			
Travelling	5	8	5			
Bank Charges		8	10			
Expenses of Meetings	3	16	0			
Typing	2	14	4			
Audit	3	3	0			
Clerical assistance	10	0	0	41	0	8
Grant						
Fresh Water Biological Association				10	0	0
Journal of Ecology. Cost *less* Sales				141	16	2
Journal of Animal Ecology. Cost *less* Sales				186	7	6
				379	4	4
Balance: Surplus for the Year, carried forward				107	9	3
				£486	13	7
Journal of Ecology, 1940:						
Cost: Paper, Blocks, Printing and Binding				647	8	9
Publishers' Commission				78	1	2
Carriage and Postages				29	4	3
Insurance of Stock				4	18	6
Advertising				1	3	3
				£760	15	11
Journal of Animal Ecology, 1940:						
Cost: Paper, Blocks, Printing and Binding				418	12	9
Publishers' Commission				40	18	1
Carriage and Postages				15	1	7
Insurance of Stock				8	1	5
Advertising					4	0
				£482	17	10

BALANCE SHEET AT 31 DECEMBER 1940

Assets

	£ s. d.	£ s d
Cash at Bank, Current Account	191 19 8	
,, ,, Deposit Account	100 0 0	
		291 19 8
Journal of Animal Ecology:		
Balance of Publishing Account for 1940, due from Cambridge University Press.		105 5 6
Stock of Paper in hand, at cost		21 6 2
Investments at cost: . .		1,268 16 10
		£1,687 8 2

Notes *re* Investments

Totals held, 31 December 1940:	£ s d
£1,050 of 3½ % War Loan at cost ...	1,070 6 10
£200 of 5 % Conversion Loan at cost	198 10 0
	£1,268 16 10

The market value of the above Investments on 31 December 1940 was:

	£ s. d.
3½ % War Loan at $103\frac{1}{16}$	1,081 18 2
5 % Conversion Loan at 108	216 0 0
	£1,297 18 2

A further Asset, not valued above, is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) V. S. SUMMERHAYES,
ALEX S. WATT,
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' subscriptions, prepaid for 1941/42, ...		7 5 0
Library Fund		1 5 0
Journal of Animal Ecology, vol **9**, No. 2		
Balance of Printing Account due		170 11 2
Sundry accounts due		7 12 0
General Revenue Account, Surplus in hand:		
Balance at 31 December 1939	1,393 5 9	
Surplus for Year 1940	107 9 3	
		1,500 15 0
		£1,687 8 2

Audited and found correct and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, Bishopsgate, London, E.C. 2.

25 *January* 1941

LIST OF MEMBERS (7 February 1941)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notiffed at once to the *Hon. Secretary*, Dr H. Godwin, Botany School, Cambridge.

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VOLUME 29 No. 2

A STUDY OF THE CARBON : NITROGEN RELATIONSHIP OF SOILS FROM THE TYPICAL CONIFEROUS FORESTS OF THE HIMALAYAS

BY R. C. HOON AND C. L. DHAWAN

(*With three Figures in the Text*)

RECENTLY a number of soil profiles under deodar (*Cedrus Deodara*), blue pine (*Pinus excelsa*), spruce (*Pinus Morinda*) and chir (*Pinus longifolia*) in the Kulu Forest Division (Punjab) were examined and described (Taylor *et al.* 1936). The results of a similar investigation with soils from another part of the Himalayan Range, viz. the Kashmir Valley, had been presented in another publication (Hoon, 1939). The two areas manifested considerable differences as regards geology, climate and the genetic development of the soil profiles. As the organic matter associated with soils is known to play an important role in the development of the soil profile it was considered of interest to study the carbon : nitrogen relationship of the soils under coniferous forests of those two areas of the Himalayas and to see how the chemical nature of humus associated with soils of the two areas compared with one another and with those in other parts of the world.

GEOGRAPHY AND GEOLOGY OF THE AREAS

The Kulu forests are situated between the north latitudes 31° 23′ and 32° 26′ and east longitudes 76° 59′ and 77° 50′. The normal annual precipitation varies from 40 to 50 in. at the rain-gauge stations and from 45 to 70 in. at higher elevations. The snowfall during winter is heavy. Maximum rainfall occurs in the months of July and August and is due to the summer monsoons. The year is characterized by two wet periods—mid-March to mid-April and July to September, the former due to the melting of snow. The principal rock formations are gneiss, shales, schists and quartzite. The majority of the soil profiles of this area belong to the podsol and brown earth groups and their main characteristics, viz. the distribution of sesquioxides, silica and organic matter, etc., are analogous to those described for similar types of profiles in other parts of the world (Hoon, 1936). However, the podsol profiles of this area are characterized by possessing a high degree of saturation of A_0 and A_1 horizons, and thus having an almost neutral reaction instead of being acidic. As will presently be shown, this high base saturation of the top horizons of the profiles plays an important part in affecting the constitution of the organic matter associated with the soils of this area.

The main Kashmir valley is situated between north latitudes 33° 30′ and 34° 30′ and east longitudes 74° and 75° 15′. The rainfall in this part occurs chiefly during the months of March and April and not during the recognized summer monsoon period as in the Kulu area. The normal annual precipitation varies from 25 to 40 in. With the exception of the months of March and April when the rainfall is supplemented by the melting of snow the rest of the year in the main Kashmir valley is dry from the point of availability of water for the flora. The climatic conditions in this part are, therefore, very much different from those prevailing in the Kulu area. The more important geological formations in this area are, first, the "Panjal Traps" which consist of thick series of pyroclastic slates, conglomerates and agglomeratic products with overlying thick series of bedded andesitic traps and, secondly, the "Karewas" which are held to be the surviving remnants of deposits of a lake which once filled the whole valley and consist of horizontally stratified deposits of bluish clayey loam. The soils derived from these two geological formations exhibit marked differences—soil derived from "Panjal Traps" being light, well drained and invariably covered with rich forests of deodar while that from "Karewas" is deep, heavy, ill-drained and covered with extensive forests of blue pine and silver fir (*Abies pindrow*). Chir is characteristically absent from this area.

A number of soil profiles from both the Kulu and Kashmir areas were selected for the present investigation. A categorical description of the type of overwood, height, aspect, slope and the ground flora, associated with each of the soil profile examined, is given in Table 1. The ground floras are given in the descending order of the frequency with which they were found growing at each of the sampling sites. It is seen that although a few types of flora do seem to be associated with soil representing some particular type of overwood, e.g. *Fragaria* and *Viola* grow more frequently on soil type preferred by deodar, etc., but, on the whole, the ground floras in the two areas are fairly different.

EXPERIMENTAL

The soils were analysed for their organic matter content, exchangeable bases, total exchange capacity and the *p*H. The organic matter associated with soils was further analysed for its carbon and nitrogen contents.

The carbon content of the organic matter associated with soils was determined according to Walkley & Black (1934), and the nitrogen content by the modified Kjeldahl's method as proposed by Bal (1925). The exchangeable bases and total exchange capacity of soils were determined by the usual methods. The degree of saturation represented the percentage proportion of the total of exchangeable sodium, potassium, calcium and magnesium to the total exchange capacity of soils. The *p*H of 1:5 soil suspensions was determined by the glass electrode. The organic matter content of soils was represented by the loss on ignition after oven-drying them at 110° C.

The results of soil analyses are given in Tables 2–4 and have been classified

Table 1. *Description of soil profiles*

Reg. no.	Area and type of profile	Type of overwood	Parent rock or material	Aspect and slope	Height in feet above sea-level	Ground flora at the site (percentage frequency in brackets)
40	Kulu (podsol)	Deodar	Mica Schist.	N.W.; moderate	7900	*Fragaria* (32·6), *Viola* (17·4), *Galium* (17·4), grasses (13·0), *Pteris* sp. (8·7), *Indigofera* sp. (6·5), *Desmodium* sp. (4·4), etc., etc.
41	,,	,,	,,	N.W.; steep	7600	*Fragaria* (40·5), *Viola* (40·5), *Berberis* (8·10), etc., etc.
60	,,	Chir	Quartzite	N.N.E.; steep	5200	Ground covered with pine needles, grass, etc., and no other characteristic ground flora
62	,,	,,	,,	S.W.; steep	5700	As in (60) above
63	,,	Blue pine	—	N.; steep	5900	Grasses and *Sarcococca* abundant and *Berberis* frequent
9	Kashmir valley (podsol)	Deodar	Panjab traps	N.E.; steep	6700	*Fragaria vesca* (62·5), *Smilax vaginata* (13·6), *Galium* sp. (5·7), *Desmodium* sp. (5·7), *Viola*, *Indigofera*, etc.
13	,,	,,	,,	E.; steep	6500	Ground flora at the site negligible, grasses, *Cannabis sativa*, *Viola*, etc., in the surround
5	,,	,,	,,	S.E.; fairly steep	6200	*Fragaria* (82·2), *Viola* (7·8), *Lespedeza* sp. (3·9)
6	,,	,,	,,	S.; steep	7900	*Fragaria* (53·0), *Viola* (18·5), *Geranium wallichianum* (8·6), *Rosa macrophylla* (6·2), *Impatiens* (6·2), *Oxalis*, *Indigofera*, etc.
57	Kulu (brown earth)	,,	Mica schist.	N.E.; moderately steep	5100	Grasses (47·6), *Salvia glutinosa* (38·1), *Lespedeza* (9·5), *Berberis* (4·8), etc., etc.
61	,,	,,	Quartzite	N.; moderately steep	5000	Grasses (abundant), *Sarcococca* and bracken fern (frequent) and *Berberis* (occasional)
55	,,	Blue pine	Soil studded with boulders	E.; steep	5000	Grasses (55·6), *Desmodium* (18·5), *Labiatae* sp. (18·5), *Fragaria* (7·4)
10	Kashmir (brown earth)	,,	Karewas	S.S.W.; fairly steep	6000	*Fragaria* (52·3), *Oxalis* sp. (17·4), *Lespedeza* sp. (9·3), *Brunella* sp. (5·8), *Viola* sp. (5·8), *Cannabis sativa* (3·5), etc., etc.
11	,,	,,	,,	S.; steep	6000	*Cannabis sativa* (45·8), *Achyranthes aspera* (25·0), *Oxalis* sp. (20·8), *Celtis australis* (4·2), etc., etc.
1	,,	,,	,,	N.; gentle	5800	*Fragaria* (52·5), *Viola* (19·6), *Geranium* sp. (9·5), *Polygonum roylei* (5·7), *Oxalis* sp. (5·1), etc., etc.
3	,,	,,	,,	S.E.; steep	7300	*Fragaria* (50·7), *Geranium* sp. (24·6), *Trifolium* sp. (10·1), *Indigofera* sp. (7·3), etc.
27	Kulu (gley)	Spruce	Free water table at 133 cm.	N.W.; steep	8500	*Pteris* sp. (32·1), *Fragaria* (15·1), *Senecio* sp. (13·2), *Polygonum* sp. (11·3), grasses (11·3), *Geranium* (9·4), etc.
15	Kashmir (gley)	Silver fir	Karewa	N.; steep	8000	*Fragaria* (39·1), maiden-hair fern (27·6), *Polygonum roylei* (6·3), *Viola* (5·2), *Impatiens* (5·2), *Oxalis* (4·2), etc., etc.
16	,,	,,	,,	N.W.; moderately steep	8500	*Oxalis* (57·0), *Valerianum* sp. (14·6), *Impatiens* (5·7), *Galium* (4·0), *Viola* (3·3), maiden-hair fern (3·3), etc., etc.

FIG. I
PODSOL PROFILES

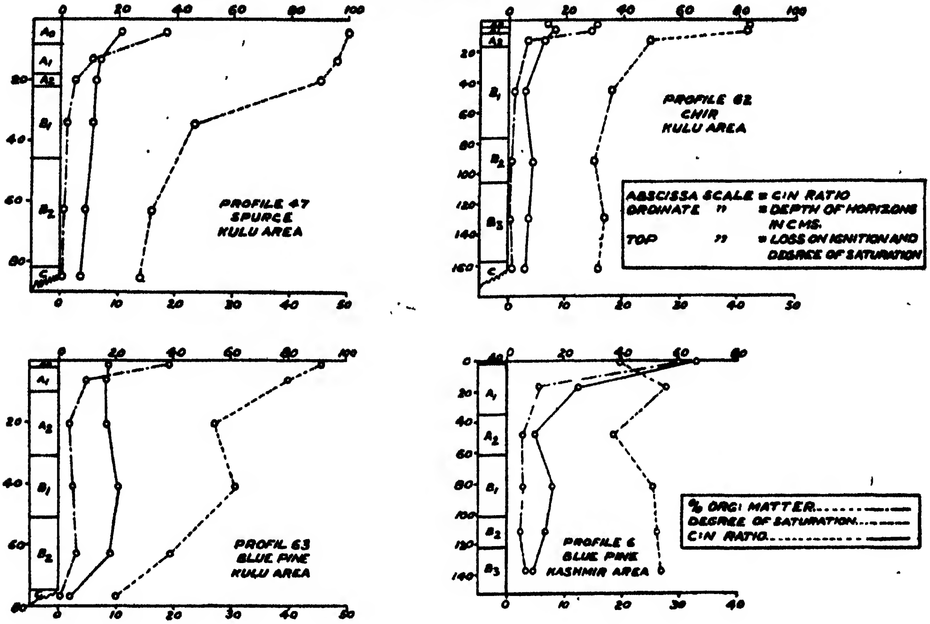


FIG. I. (CONTD)

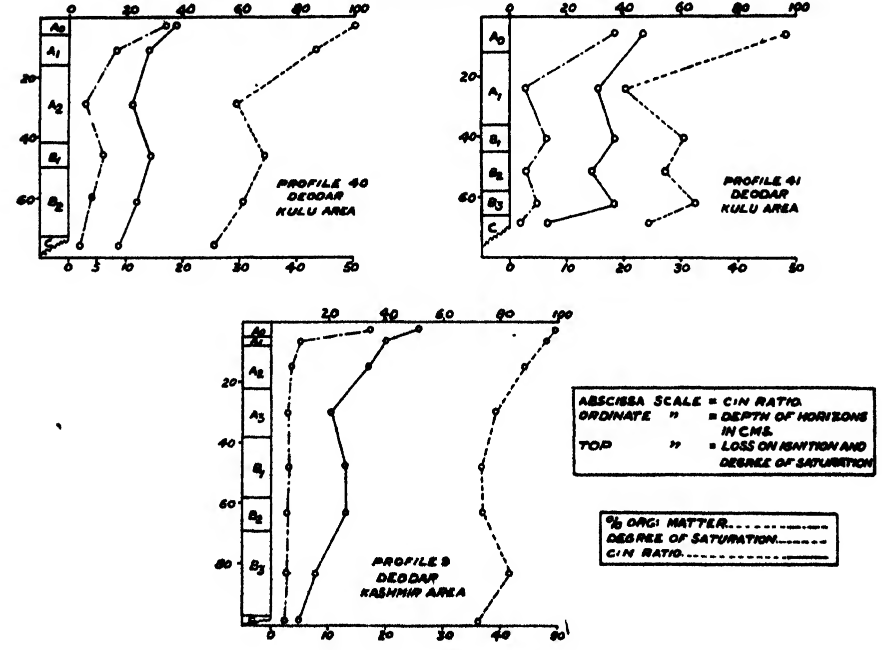


FIG. 2

BROWN EARTH PROFILES

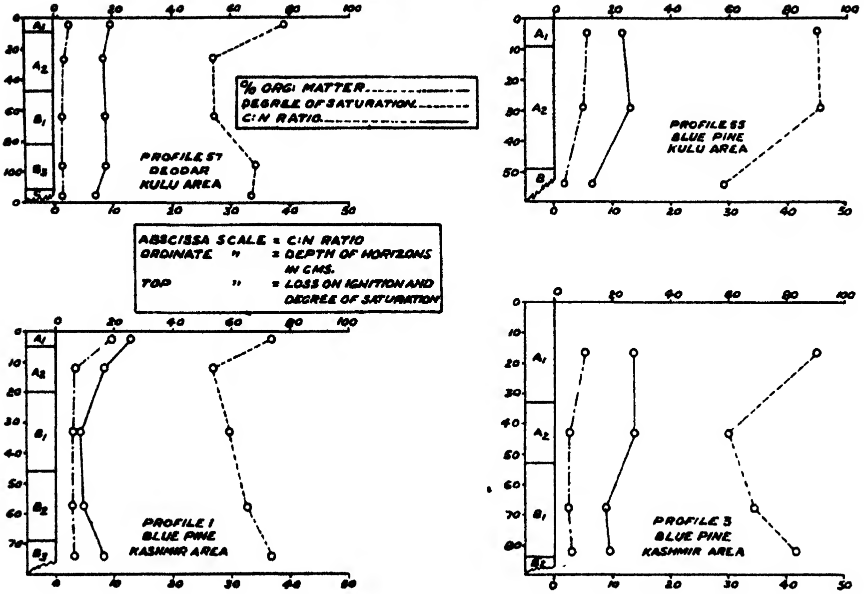
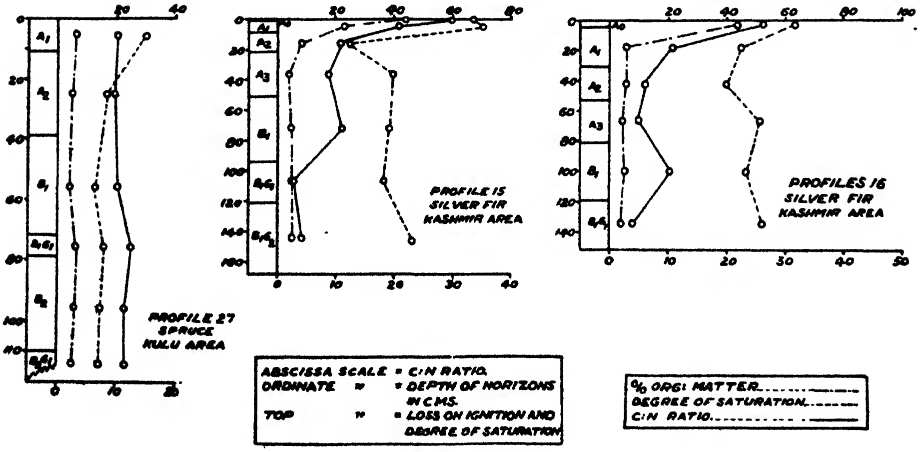


FIG. 3

GLEY PROFILES



according to the groups, viz. podsol, brown earth and gley, which any particular soil profile was found to represent on the basis of more detailed work previously reported. In order to facilitate comparison, the results of carbon : nitrogen ratio, percentage organic matter and degree of saturation of the various horizons of the soil profiles have been plotted in Figs. 1–3. To reduce the size of the diagrams the results of the percentage organic matter and degree of saturation are represented on the scale given on the top and those of carbon : nitrogen ratio on the scale at the bottom of each figure respectively. The ordinate scale represents the depth of the various horizons of the soil profile.

DISCUSSION

Although the number of soil profiles representing certain types of overwood may not be considered sufficient to justify very definite generalizations, the results, on the whole, are still of considerable interest.

Broadly speaking, the carbon : nitrogen ratios of the soils show a fair divergence between the soil profiles belonging to the different groups, viz. podsol, brown earth, etc., and to some extent amongst the soil profiles representing the same type of overwood.

One method of comparing the various soil profiles was on the basis of the mean carbon : nitrogen ratios of the complete soil profiles as done by Leighty & Shorey (1930). If the soil profiles, representing the various forest crops, were arranged in the decreasing order of their mean carbon : nitrogen ratios the following arrangement is obtained:

Kulu area: deodar > blue pine > spruce > chir;
Kashmir area: deodar > blue pine > silver fir.

It is interesting to note that in both the areas the soil profiles representing deodar have the widest carbon : nitrogen ratio, next in order come the soil profiles from blue pine areas and then those representing spruce or silver fir. As the latter areas are situated at a comparatively higher altitude or cooler aspects than those under deodar or blue pine they might be expected to receive more annual precipitation which would result in a rather wider carbon : nitrogen ratio. These soils were, however, found to have a relatively higher nitrogen content (see Tables 2–4) which accounted for the narrow carbon : nitrogen ratio of these soil profiles. The high nitrogen content of soils, representing spruce or silver fir may be attributed to the comparatively lower temperatures in those areas. Jenny (1930) showed that, provided the rainfall : evaporation ratio is constant for every 10° C. decrease in the mean annual temperature, there occurs two or threefold increase in the average nitrogen content.

Chir is conspicuously absent in the main Kashmir valley. In Kulu, chir is found to grow at comparatively lower elevations and hotter aspects. The soil under chir contains big boulders and is consequently thin. Moreover, there is no characteristic ground flora associated with this type of overwood,

Table 2. *Carbon : nitrogen ratio of the soil profiles (belonging to podsol group)*

No. of profile, type of vegetation and area	Horizon	Depths in cm.	*p*H	% Organic matter	% carbon	% nitrogen	C : N ratio	Average of C : N ratio	Degree of saturation
Profile 40 under deodar (Kulu area)	A_0	0–6	6·95	33·56	16·92	0·91	18·59	13·13	100
	A_1	6–16	6·43	16·53	7·52	0·54	14·03		86·50
	A_2	16–42	5·97	5·91	1·89	0·17	11·11		50·86
	B_1	42–50	6·46	12·13	4·86	0·34	14·29		68·76
	B_2	50–73	6·33	8·19	2·40	0·20	12·00		61·08
	C	Below 73	6·13	4·03	1·14	0·13	8·77		51·23
Profile 41 under deodar (Kulu area)	A_0	0–12	6·07	36·75	18·20	0·78	23·42	16·12	96·55
	A_1	12–36	5·24	5·42	2·55	0·17	15·45		40·71
	B_1	36–45	5·78	13·46	6·05	0·33	18·47		61·11
	B_2	45–58	5·68	5·97	2·17	0·15	14·46		54·49
	B_3	58–66	5·87	9·75	3·76	0·21	18·25		64·96
	C	Below 66	5·74	3·72	0·74	0·11	6·66		48·60
Profile 60 under chir (Kulu area)	A_0	0–4	6·54	28·59	8·24	0·73	11·27	6·74	92·57
	A_1	4–19	6·38	9·15	2·70	0·28	9·60		85·53
	A_2	19–70	6·85	0·47	0·12	0·04	3·10		33·95
	B	70–120	6·30	0·80	0·15	0·05	3·00		27·99
Profile 62 under chir (Kulu area)	A_0	0–4	6·40	30·84	9·39	0·69	13·55	9·98	83·56
	A_1	4–8	6·33	28·79	9·04	0·57	15·95		82·88
	A_2	8–17	6·07	6·83	1·68	0·14	12·45		49·13
	B_1	17–77	6·33	2·28	0·34	0·06	5·66		36·00
	B_2	77–106	6·69	1·12	0·17	0·02	8·50		30·00
	B_3	106–158	6·66	0·70	0·15	0·02	7·50		33·68
	C	Below 158	6·30	1·61	0·25	0·04	6·25		31·88
Profile 63 under blue pine (Kulu area)	A_0	0–2	6·69	38·72	19·23	1·089	17·65	15·74	91·53
	A_1	2–10	6·64	9·65	4·16	0·088	16·63		79·70
	A_2	10–31	6·18	4·06	1·48	0·087	17·01		54·24
	B_1	31–51	6·41	4·74	1·87	0·090	20·77		61·57
	B_2	51–75	5·06	6·40	2·42	0·132	18·33		38·85
	C	Below 75	5·54	0·93	0·11	0·027	4·07		20·00
Profile 47 under spruce (Kulu area)	A_0	0–8	6·70	36·42	11·046	1·06	10·41	6·68	100
	A_1	8–18	6·83	11·16	3·763	0·553	6·805		96·16
	A_2	18–22	6·27	4·96	1·686	0·281	6·00		90·38
	B_1	22–46	5·45	2·16	0·518	0·092	5·63		46·38
	B_2	46–82	5·05	1·28	0·355	0·083	4·28		31·82
	C	Below 82	4·69	0·58	0·266	0·076	3·50		27·43
Profile 9 under deodar (Kashmir area)	A_0	0–5	6·58	34·50	17·92	0·697	25·71	13·98	99·26
	A_1	5–8	6·82	10·22	3·249	0·162	20·06		96·26
	A_2	8–22	6·68	7·22	1·069	0·063	17·13		88·35
	A_3	22–38	6·38	5·91	0·536	0·051	10·50		78·10
	B_1	38–58	6·33	6·24	0·534	0·041	13·02		73·50
	B_2	58–69	6·24	5·82	0·563	0·043	13·09		73·67
	B_3	69–97	6·24	5·59	0·518	0·068	7·62		83·26
	C	Below 97	6·28	4·90	0·195	0·041	4·77		72·15
Profile 13 under deodar (Kashmir area)	A_0	0–5	7·17	40·90	18·88	0·616	30·66	21·60	85·53
	A_1	5–28	7·17	25·66	12·80	0·752	17·02		86·70
	B	28–114	5·74	6·34	1·665	0·062	26·85		41·78
	C	Below 114	6·04	6·31	0·760	0·064	11·87		85·77
Profile 5 under blue pine (Kashmir area)	A_0	0–1·5	6·61	54·70	30·21	1·00	30·21	16·94	92·72
	A_1	1·5–11	6·71	16·10	7·284	0·372	19·58		82·07
	A_2	11–42	6·28	5·42	1·155	0·049	23·57		78·16
	B_1	42–89	6·18	4·67	0·398	0·062	6·42		73·32
	B_2	89–152	6·45	4·43	0·255	0·052	4·90		89·62
Profile 6 under blue pine (Kashmir area)	A_0	0–2·5	5·96	60·10	30·76	0·935	32·90	11·62	39·47
	A_1	2·5–43	5·73	11·45	4·67	0·370	12·62		50·56
	A_2	43–62·0	5·93	5·70	0·50	0·102	4·90		37·15
	B_1	62·0–102	5·86	5·65	0·502	0·062	8·09		50·97
	B_2	102–122	5·63	4·67	0·407	0·061	6·66		52·32
	B_3	122–152	5·93	6·72	0·367	0·081	4·53		53·70

Table 3. *Carbon : nitrogen ratio of the soil profile (belonging to brown-earth group)*

No. of profile, type of vegetation and area	Horizon	Depth in cm.	*p*H	% organic matter	% carbon	% nitrogen	C : N ratio	Average value of C : N ratio	Degree of saturation
Profile 57 under deodar (Kulu area)	A_1	0–9	6·93	5·26	1·46	0·153	9·55	8·43	78·74
	A_2	9–48	6·04	3·54	0·73	0·088	8·28		53·84
	B_1	48–82	5·75	2·87	0·56	0·064	8·72		54·32
	B_2	82–112	6·05	2·68	0·54	0·062	8·66		68·29
	C	Below 112	6·33	2·81	0·30	0·043	6·92		67·00
Profile 61 under deodar (Kulu area)	A_1	0–5	6·89	29·64	14·94	0·278	53·63	19·08	98·47
	A_2	5–13	4·93	3·87	1·58	0·118	13·36		32·38
	A_3	13–23	5·45	2·56	0·98	0·087	13·46		41·15
	B_1	23–32	5·85	2·41	0·86	0·072	11·81		51·49
	B_2	32–98	5·82	2·12	0·74	0·080	9·19		48·48
	B_3	98–110	5·58	6·87	3·03	0·125	24·18		57·32
	C	Below 110	5·54	2·07	0·54	0·067	7·95		39·61
Profile 55 under blue pine (Kulu area)	A_1	0–9	6·49	11·12	3·29	0·283	11·63	10·30	89·89
	A_2	9–49	6·36	9·76	2·79	0·216	12·92		91·06
	B	Below 49	6·10	3·20	0·75	0·118	6·35		57·95
Profile 10 under deodar (Kashmir area)	A_1	0–9	6·99	9·28	3·009	0·085	35·40	21·30	70·70
	A_2	9–24	6·61	6·28	0·76	0·074	10·27		73·36
	B_1	24–50	6·64	7·47	0·408	0·034	12·00		82·92
	B_2	50–75	6·54	5·22	0·312	0·019	16·42		69·77
	C	Below 75	6·74	5·01	0·248	0·045	5·51		71·19
Profile 11 under deodar (Kashmir area)	A_1	0–9	7·11	19·71	9·954	0·488	20·35	32·52	91·40
	A_2	9–32	6·57	6·60	1·256	0·041	30·63		70·62
	B	32–52	6·74	5·89	2·973	0·061	48·73		76·76
	C	52–107	6·03	5·95	1·920	0·048	40·00		70·31
Profile 1 under blue pine (Kashmir area)	A_1	0–5	6·17	19·15	9·48	0·743	12·76	7·58	73·60
	A_2	5–20	6·14	6·76	1·524	0·183	8·33		53·60
	B_1	20–46	6·20	6·05	0·413	0·099	4·18		59·17
	B_2	46–69	6·46	6·56	0·603	0·130	4·64		65·18
	B_3	69–152	6·76	6·30	0·794	0·099	8·02		73·84
Profile 3 under blue pine (Kashmir area)	A_1	0–33	6·00	10·56	4·656	0·340	13·69	11·47	90·30
	A_2	33–53	6·00	5·27	1·116	0·081	13·78		60·15
	B_1	53–84	6·13	5·02	0·740	0·084	8·81		68·67
	B_2	84–114	6·28	6·05	1·088	0·113	9·63		83·18

Table 4. *Carbon : nitrogen ratio of the soil profiles (belonging to gley type)*

No. of profile, type of vegetation and area	Horizon	Depths in cm.	*p*H	% organic matter	% carbon	% nitrogen	C : N ratio	Average value of C : N ratio	Degree of saturation
Profile 27 under spruce (Kulu area)	A_1	0–11	4·60	5·97	2·61	0·255	10·02	10·84	29·73
	A_2	11–39	4·74	4·69	1·62	0·169	9·53		16·59
	B_1	39–62	4·71	3·76	1·15	0·113	10·17		12·56
	B_1, G_1	62–69	4·71	6·31	2·23	0·180	12·39		15·80
	B_2	69–110	4·89	5·65	2·00	0·176	11·36		14·62
	B_2, G_1	Below 110	4·99	4·93	1·78	0·155	11·57		14·24
Profile 15 under silver fir (Kashmir area)	A_0	0–1·3	6·17	43·45	23·82	0·802	29·70	12·48	65·84
	A_1	1·3–9	5·46	22·57	12·035	0·582	20·63		70·04
	A_2	9–22	4·75	8·21	1·984	0·187	10·61		24·44
	A_3	22–51	5·07	3·94	0·522	0·060	8·70		39·19
	B_1	51–94	4·85	4·52	0·284	0·026	10·92		37·94
	B_1, G_1	94–131	5·05	4·80	0·237	0·088	2·69		36·19
	B_1, G_2	131–168	4·98	5·14	0·164	0·040	4·10		46·08
Profile 16 under silver fir (Kashmir area)	A_0	0–5	5·91	43·55	25·53	0·976	26·16	10·28	63·35
	A_1	5–31	5·86	5·49	0·682	0·065	10·46		44·85
	A_2	31–53	5·19	5·62	0·680	0·116	5·86		39·90
	A_3	53–81	5·09	4·30	0·350	0·073	4·79		51·42
	B_1	81–119	5·19	5·09	0·540	0·052	10·38		46·74
	B_1, G_1	119–15	25·48	4·22	0·268	0·066	4·04		52·34

i.e. the ground is mainly covered with a litter of pine needles and grass. All these facts contribute to maintain the mean carbon-nitrogen ratio of these soil profiles even below 10. This point, however, needs further elucidation as the number of soil profiles representing chir which were examined was quite small.

The carbon : nitrogen ratios of the surface horizons is high in almost all the profiles and there is invariably a narrowing of the ratio as depth of soil increases. The comparatively wider ratios of the surface horizons is due to the presence of undecomposed plant remains while the organic matter in the lower horizons is in an advanced stage of decomposition (Dyer, 1902) and Leighty & Shorey (1930).

In the majority of soil profiles there is an accumulation of nitrogen in the B horizons. It is very prominent in the soil profiles of the podsol group and is due to the mobility of the nitrogenous humus constituents from the surface layers. Similar observations were made by Weis (1929, 1932) in his study of heath podsols.

Broadly speaking, therefore, the results of the carbon : nitrogen ratios obtained for the soil profiles of both the Kulu and Kashmir areas are analogous to those reported for soils in other parts of the world. One point of contrast is, however, worth mentioning. Joffe & Watson (1932) found a fairly wide carbon : nitrogen ratio in the top horizons of the podsol profiles examined by them, i.e. 49·3 and 49·9 in the A horizons. Although the carbon : nitrogen ratios of the A_0 horizons of the various profiles, reported in this paper, is high the values do not approach those given above. There is, moreover, a definite narrowing of the ratio in the A_1 horizons. This difference is rather fundamental. It is, however, possible to afford an explanation of this difference on the basis of the high base saturation of the top horizons of the Himalayan soil profiles. An increase in the base content of the plant residue is known to be favourable to an increase in the rate of decomposition of the organic matter resulting in the formation of humus which is richer in nitrogen and less acid in reaction (Powers, 1932). The high acidity of the soils had been shown to be one of the factors responsible for the wide carbon : nitrogen ratio of the Alpine soils (Wasowicz, 1933).

The effect of the base saturation on the carbon : nitrogen relationship receives further confirmation when the differences of the carbon : nitrogen ratios of the two sets of soil profiles from the Kulu and Kashmir areas are compared with one another. The A_0 and A_1 horizons of the Kulu soil profiles have a higher degree of saturation than the corresponding horizons of the Kashmir soil profiles. A statement showing the average values of the carbon : nitrogen ratios and the degree of saturation of the two top horizons of the Kulu and Kashmir soil profiles is given below (Table 5).

It is seen from this table that the carbon : nitrogen ratios of the Kashmir profiles, which have comparatively a lower degree of saturation, are wider than those of Kulu area.

Table 5

Type of overwood	Horizon	Kulu		Main Kashmir valley	
		Mean degree of saturation	Mean C : N ratio	Mean degree of saturation	Mean C : N ratio
Deodar	A_0	98·28	21·00	77·71	31·87
	A_1	76·10	25·75	86·26	23·21
Blue pine	A_0	91·53	11·65	66·10	31·55
	A_1	84·80	14·13	74·14	14·67
Spruce	A_0	100·00	10·41	—	—
	A_1	62·95	12·77	—	—
Silver fir	A_0	—	—	64·59	27·93
	A_1	—	—	57·45	15·57
Chir	A_0	88·07	12·41	—	—
	A_1	84·21	12·77	—	—

Profile 61 (Kulu area) seems to be rather an exception. It has no peat layer, but the organic matter content of the A_1 horizon is fairly high, being almost of the order of that of A_0 horizon in many of the soil profiles of the podsol group. There is, however, a sharp decrease in the organic matter content of the next horizon.

Profile 57 (Kulu area) has a very low carbon : nitrogen ratio in the top horizon, and there is not much of variation up to the C horizon. The overwood at this site consisted of deodar poles about 75–80 years old, but the area had been overgrazed in the past and the number of ill-formed trees was very large. The narrow carbon : nitrogen ratio in this profile might be attributed to overgrazing.

GLEY PROFILES

In the gley horizons there is usually an increase in the nitrogen content which results in a comparatively narrower carbon : nitrogen ratio. It is likely that the proximity of the water table contributes to the accumulation of nitrogenous content in these horizons. This point needs further investigation.

SUMMARY

A number of the Himalayan soil profiles belonging to the podsol, brown earth and gley types and under different forest crops have been examined for their carbon and nitrogen contents, *p*H, organic matter and degree of saturation. It is brought out that the top horizons have fairly high carbon : nitrogen ratios which, however, narrow with the depth of the soil profiles. The soil profiles representing deodar have comparatively the widest mean carbon : nitrogen ratio, next come the profiles representing blue pine and finally those taken from spruce or silver fir areas. The horizons of illuviation and the gley horizons manifest an increase in the nitrogen content which results in a narrow carbon : nitrogen ratio of these horizons.

It is brought out as a result of this investigation that, in general, the carbon : nitrogen relationship of the soils, examined, are analogous to those reported for soils in other parts of the world except that the carbon : nitrogen ratios of the top horizons of these profiles are not of the same high order. This difference is attributed to the comparatively higher base saturation and almost neutral reaction of the top horizons of the soil profiles discussed in this paper.

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THE CONTROL OF THE NUMBERS OF FRESH-WATER PHYTOPLANKTON BY SMALL INVERTEBRATE ANIMALS

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(*With one Figure in the Text*)

INTRODUCTION

DURING work on the growth of algae in experimental tubs, it was found that when certain small planktonic animals became numerous, their feeding had very striking effects on the numbers of algae and on the general conditions in the tub. Similar effects were later observed in ponds. The importance of the phytoplankton, including the nannoplankton, as a source of food for rotifers and Cladocera, is generally recognized, but it is perhaps not so widely realized how seriously these small animals can reduce the numbers of the phytoplankton. Dieffenbach & Sachse (1912), working on the biology of rotifers in ponds, noted that a rich growth of planktonic algae was frequently followed by a great increase in the number of rotifers, which fed on the algae and rapidly reduced their numbers. When the food supply was exhausted, the number of rotifers decreased. The experiments which will be described in this paper suggest that factors other than the exhaustion of the food supply may be involved in such a cycle of events.

An outline of the sequence of events as observed in many tubs will be given first, and followed by a more detailed account of experimental work on the subject.

The tubs were half wine casks, of approximately 100 l. capacity. At the beginning of each experiment, each tub was sterilized with approximately $N/10$ sulphuric acid, neutralized and washed, so that no inoculum of algae or animals remained from previous experiments. The tubs were then filled with a rich culture solution, the composition of which is given in the Appendix, and inoculated with a mixed culture of algae from ponds or from other tubs. All tubs were open to inoculation by wind-borne spores, etc., and by accidental contamination, e.g. from birds coming to drink. The algae multiplied rapidly, the rate of increase varying with the season, until a fairly constant level was reached. The dominant algae of the plankton were nearly always small members of the Chlorococcales—*Chlorella*, *Scenedesmus*, or a minute alga which has been described (Pennington, 1941), under the name of *Diogenes rotundus*, and which, apart from its method of reproduction, resembles a small *Chlorella*.

At the time when the population of a tub had reached a high, more or less constant, level, *Diogenes rotundus* almost invariably formed the bulk of the phytoplankton, and in bright summer weather its numbers often exceeded 20,000 per cu. mm., when the water would be bright green and almost opaque. In such a tub, it was frequently observed that in the course of a few days the colour changed from bright green to a dull olive green, and then to black, and at the same time became sufficiently clear to show the bottom of the tub. Counts of the algae showed that their numbers had decreased very rapidly, and on examination, the water was found to contain enormous numbers of small animals—in every case either the rotifer, *Brachionus pala*, or the crustacean, *Daphnia pulex*. This sudden destruction of the algae by small invertebrate animals is here termed a 'massacre'.

EXPERIMENTAL WORK

When the significance of the 'massacre' phenomenon was appreciated, further investigations of the feeding habits of small animals from the tubs were carried out. The gut contents were examined, and those species which appeared to feed on plankton algae were kept and observed in cultures in beakers. Then closer investigations were made of their feeding habits in the tubs, and the course of a massacre followed in detail.

(1) *Gut contents*

Of all the small animals whose gut contents were investigated, it appeared that only rotifers and *Daphnia* were important in reducing the numbers of plankton algae. *Brachionus pala* and *Daphnia pulex* both had large numbers of the smaller plankton algae from the tubs in their stomachs—in fact, these algae appeared to be their main diet in the tub environment. Live individuals of *Brachionus pala* in a culture of *Diogenes* were observed to take in large numbers of the algae by the action of the cilia on their trochal disks. Once eaten by a rotifer, the algae fairly rapidly became unrecognizable, only the somewhat misshapen cell wall surviving digestion. In the gut of *Daphnia*, the algae retained their shape over a longer period. Neither of these animals appeared to show any selectivity in feeding, apart from that imposed by the relative sizes of animals and algae. *Brachionus* ate *Chlorella* as well as *Diogenes rotundus*, when both were present, but nothing larger. *Daphnia* ate any alga occurring in the cultures in which it was grown, up to the size of *Pediastrum Boryanum*, small individuals of which were found in its gut.

The other animals commonly present in the tubs were not important in reducing the numbers of plankton algae. The only other plankton feeder was the larva of *Culex* sp., which was frequent in the summer. The guts of these were full of plankton algae, but the larvae did not occur in sufficiently large numbers to cause an appreciable reduction in the numbers of algae in the tub.

Protozoa which fed on plankton algae were always present and sometimes frequent in the tubs, but they ate only very small quantities, and there was never any evidence of their having any serious effect on the numbers of algae in the tubs.

Red *Chironomus* larvae (bloodworms) were abundant on the sides and bottom of the tubs. These fed partly on the rather sparse growth of filamentous algae, but chiefly on the sediment which collected on the bottom of the tubs. This sediment was composed largely of living and dead algae. The gut contents of these larvae consisted almost entirely of filaments and algal sediment. When the larvae were washed free of sediment, and placed in a culture of planktonic algae, they were quite unable to feed on the plankton, and starved.

(2) *Experiments in beakers*

Having proved that rotifers and *Daphnia* can eat the algae which occurred in the tubs, experiments were carried out to see if these animals could reduce the numbers of algae in a culture. *Brachionus pala* and *Daphnia pulex* can both live well in beakers for some days. The animals were obtained by filtering tub water, and were added in fairly large numbers to beakers containing a suspension of algae of known concentration. A similar beaker of algal suspension was kept under similar conditions as a control. At the end of the experiment, the algae in samples from the beakers with animals and from the control were counted. The results of some of these experiments were as follows:

Experiment 1. *Daphnia pulex*

	Beginning of the experiment		After 24 hr.	
	No. in control	No. in beaker to which *Daphnia* added	No. in control	No. in beaker to which *Daphnia* added
Chlamydomonas sp.:				
No. per cu. mm.	51	40	44	0
No. counted	51	40	44	0
Factor	1	1	1	—

Experiment 2. *Daphnia pulex* and *Brachionus pala*

(The alga in each case is *Diogenes rotundus*.)

	Numbers of *D. rotundus* on the following days				
	1	2	4	5	6
1. Control:					
No. per cu. mm.	4133	5465	6000	8200	10,666
No. counted	124	82	90	123	80
Factor	100/3	200/3	200/3	200/3	400/3
2. With 100 *Daphnia* per 100 c.c.:					
No. per cu. mm.	4565	4260	733	383	103
No. counted	137	64	22	23	77
Factor	100/3	200/3	100/3	50/3	4/3
3. With 1700 rotifers per 100 c.c.:					
No. per cu. mm.	4765	5200	5133	6333	7200
No. counted	143	78	77	95	108
Factor	100/3	200/3	200/3	200/3	200/3

The 'Factor' quoted in the above table is the number by which it was necessary to multiply the number of algae counted, in order to convert it to number per cubic millimetre. In both experiments, the numbers of other algae were insignificant.

These experiments show that the feeding of *Daphnia pulex*, when in large numbers, can reduce the numbers of algae in a suspension very considerably. *Brachionus pala* did not actually reduce the numbers of algae, but prevented them from rising as high as in the control. In all cases, at the end of the experiment large numbers of the algae from the suspension were found in the animals' guts.

(3) *Experiments on tubs*

The next step was to find out whether a massacre could be produced experimentally in a tub, by the addition of small animals. In May 1939, two tubs, A and B, were sterilized, as previously described, washed, filled with culture solution, and inoculated with algae. The numbers of algae were followed by daily counts in triplicate, and frequent sampling showed that the water of the tubs was almost free from rotifers. Fig. 1 shows the rise in numbers of *Diogenes rotundus* (by far the most abundant alga), at first following an exponential course, and then falling off until a fairly constant high level was reached and maintained. The behaviour of the two tubs was very similar. The oxygen content of the water was followed by daily determinations of dissolved oxygen by the Winkler method. After six weeks, when the numbers of algae were 14,375 and 10,250 per cu. mm. in A and B respectively, a large number of rotifers was introduced into B. After this inoculation, there were thirty-eight rotifers per c.c. in B, and none in A.

Fig. 1, in which the mean of the three daily counts of *Diogenes rotundus* is plotted, shows that the inoculation with rotifers was followed by a very rapid decrease in the numbers of *Diogenes* in B, while the numbers in the control A remained high. After 12 days, the numbers of *Diogenes* in B had fallen from 10,250 to 1600 per cu. mm., and the gut contents of the rotifers consisted largely of *Diogenes*. By this time, many of the rotifers in B had died, presumably from lack of oxygen, since 9 days after the inoculation the oxygen concentration in B had fallen to zero. The tub B showed all the characteristic features of a massacre—the colour changing from bright green to olive, then to black, and the water becoming clear. The black colour is possibly due to ferrous sulphide, and is apparently associated with the very low oxygen concentration which is an invariable feature of a massacre, presumably because of the removal of algae from the water and the presence of large quantities of easily oxidizable organic matter.

At this stage of the massacre in tub B, the rotifers first swam to the surface, and soon after all died, apparently from asphyxiation. Meanwhile, the numbers of *Diogenes* were rising rapidly, and in a short time reached and exceeded the

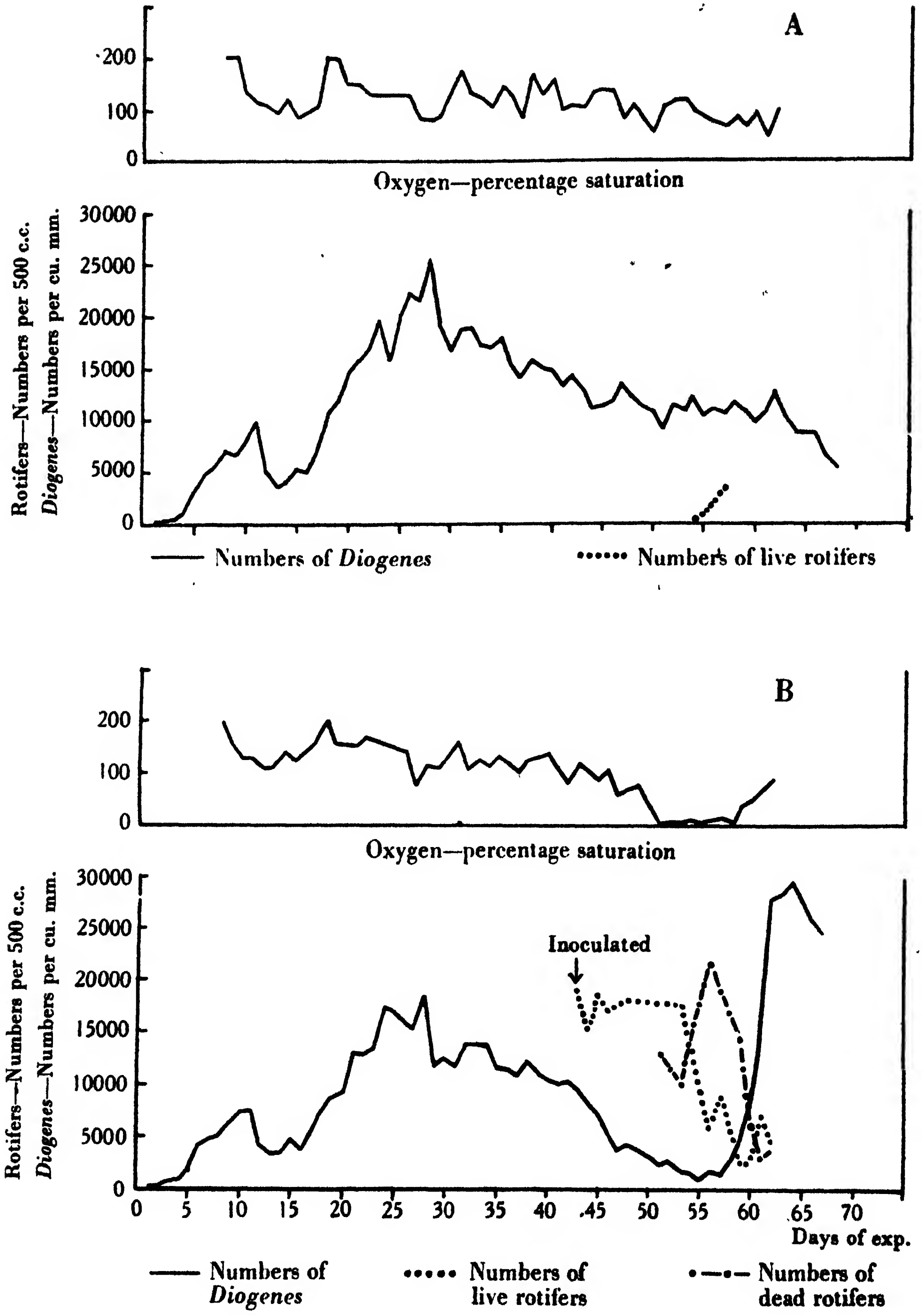

Fig. 1. Graphs of the numbers of *Diogenes rotundus*, numbers of live and dead rotifers, and the percentage saturation of oxygen, in tubs A and B, during the experiment described on p. 207.

numbers previous to the rotifer inoculation. The oxygen concentration increased at the same time.

The sequence of events in tub B therefore shows the full story of an experimentally induced massacre by rotifers, death of rotifers, presumably from asphyxiation, and recovery of algae from the massacre. A similar sequence of events was repeatedly observed in massacres which arose spontaneously in tubs. Sometimes the massacres were caused by *Daphnia pulex*, and these followed an exactly similar course. A massacre occurred sooner or later in the history of most tubs, but the time of its occurrence varied considerably. In summer, it generally took place a few weeks after the inoculation, but in winter all processes were slower, and the period which elapsed before the massacre was longer.

DISCUSSION

Importance of plankton-feeding animals in the control of the numbers of the phytoplankton

From these experiments, it is obvious that plankton-feeding animals can have striking effects on the numbers of the phytoplankton. The course of events depends on the relative numbers of animals and algae present. It appears that when the numbers of algae are still small, a relatively small number of animals may prevent any effective increase in algal numbers. It is believed that this is what took place in several tubs in which the algal inoculum failed to grow and disappeared.

Once the algae have begun to increase, the sequence of events here described as a massacre begins. In the first phase there is a steady increase in the numbers of algae, their reproduction rate being more than sufficient to compensate for the numbers eaten by animals. The reproduction rate of the algae then slows down, a critical stage being reached when this reproduction rate is such that the daily increase in numbers is just balanced by the numbers consumed by animals. Further increase in the number of animals at this stage results in a massacre, in which the numbers of algae are very rapidly reduced, until nearly all have been destroyed. This produces important changes in water composition, notably almost complete oxygen depletion, as a result of which the animals are frequently destroyed. The few remaining algae are not destroyed, and after the death of the animals begin to multiply rapidly once more.

The time at which the critical stage is reached is rarely the same, even in tubs which have been sterilized together and have subsequently received exactly similar treatment. This is thought to be due to differences, from one tub to another, in the respective reproduction rates of animals and algae. The factors controlling these reproduction rates are still largely unknown. Sometimes the critical stage was reached very soon after inoculation, before the numbers of algae were very high, and here there was no sudden asphyxiation of the animal population, but only a gradual disappearance, apparently from starvation, following the disappearance of the algae.

Before the importance of thorough sterilization of tubs was realized, the differences, in growth of algae, between similarly treated but unsterilized tubs were very considerable. While no direct proof can be offered, it seems likely that these differences were due to variation in the animal population, arising from chance inoculation with animals from previous experiments. When the tubs were sterilized by the sulphuric acid method, these variations in behaviour were very much reduced.

Phenomena similar to those which have been described from the experimental tubs have been observed in the field. In the rich culture solution of the tubs, both animals and algae were present in greater concentration than is usually found in ponds, but there seems no reason why similar massacres should not occur in eutrophic ponds. An instance of such a massacre was observed in a pond near Burghfield Common, Reading, in the autumn of 1938. A rich growth of algae, chiefly flagellates, developed in the water, and then suddenly disappeared, its disappearance coinciding with the appearance of large numbers of a Cladoceran (probably *Daphnia* sp.) and a Copepod. At the same time, the water became black and acquired a foul smell, typical of anaerobic waters. This late phase of a massacre, in which the zooplankton is concentrated in the upper layers of the water, which are more oxygenated, and algae have practically disappeared from the water, is common in farm ponds.

Variations in the growth of algae in similarly treated tubs have been explained as being probably due to chance variation in the number of plankton-feeding animals. A similar explanation might account for the great differences which have been observed between the flora of several ponds in the same field, where it would appear that the general environment is similar for all the ponds.

In tubs, the effects of plankton-feeding animals on the phytoplankton showed no relation to season. In ponds, the appearance characteristic of a massacre may occur at the same season for several years, but this is probably only a subsidiary effect of marked seasonal changes, particularly the drying up in summer. In itself, the massacre cycle appears to have no relation to season.

SUMMARY

The plankton-feeding animals *Brachionus pala* and *Daphnia pulex*, when present in sufficient numbers, can reduce the numbers of the phytoplankton very rapidly. In all cases observed, such a rapid reduction of the phytoplankton was accompanied by almost complete oxygen depletion, and death of the animals, after which the numbers of algae again increased. This cycle of events, first observed in experimental tubs, has been found to occur in ponds. It is suggested that in addition to such rapid and sudden reduction in numbers of

algae, plankton-feeding animals may have important effects on the rate of increase in numbers of algae at any stage of the annual cycle.

I wish to thank Prof. T. M. Harris for his continued help and criticism throughout this work and the preparation of this paper.

APPENDIX

Composition of the culture solution in the experimental tubs

Each tub contained approximately 100 litres of Reading tap water.

All the tubs contained the following salts:

Calcium carbonate, 0·1 g./l.
Calcium phosphate, 0·05 g./l.
Potassium sulphate, 0·05 g./l.
Magnesium sulphate, 0·05 g./l.

In addition, each tub contained *one* of the following sources of nitrogen:

Ammonium sulphate, 0·3 g./l.
Potassium nitrate, 0·3 g./l.
Ammonium nitrate, 0·15 g./l.

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NOTE ON THE STATUS OF SALT-MARSH VEGETATION AND THE CONCEPT OF 'FORMATION'

By A. G. TANSLEY

In Dr V. J. Chapman's most interesting and valuable survey of the types of British salt-marsh vegetation published in the last issue of this *Journal* (Studies in salt-marsh ecology, VIII, *J. Ecol.* **29**, 69–82, 1941) the author dissents (p. 69) from my description of this vegetation as a 'formation' (*The British Islands and their Vegetation*, Chap. XL), which, as he says, I describe as representing a 'climax' in the conditions under which it exists. In regard to the *identification* of 'climax' with 'formation' I shall have something to say later in this note. Dr Chapman goes on to say: 'Salt-marsh vegetation is essentially dynamic', and he indicates that 'where fresh water flows out to sea there would seem little doubt that salt marsh progresses to reed swamp, and further development by way of carr to the woodland climax is theoretically possible'. He believes, with Godwin, 'that the fens have developed in this manner', and that 'if the land is rising in relation to sea-level, then sooner or later the halophytic vegetation will give way to normal land vegetation...'.

With all this I have no quarrel whatever. It is true that I have never found evidence in the British Isles that salt marsh passes normally into 'land vegetation', but it is a perfectly legitimate and indeed inevitable inference that, if fresh water replaces salt water, fresh-water marsh or reed swamp will supervene, and that if the surface of the land rises above the ground water-level, terrestrial vegetation, culminating in the climatic climax, will be initiated. Such developments I regard as changes from one formation to another (cf. *op. cit.* p. vii, where the change from reed swamp to land vegetation is instanced). Meanwhile salt-marsh vegetation *does* represent a climax 'in the conditions under which it exists'. These conditions are of course the presence of salt water as the master factor and the ebb and flow of the tides. And salt-marsh vegetation shows, conspicuously enough, the correspondence of characteristic life forms with positions of relative equilibrium on which I insisted. As soon as the decisive factors of salt water and tidal flow are withdrawn the salt-marsh formation is replaced by something else. In other words the change from salt marsh to fresh-water or land vegetation is not autogenic succession but is determined by allogenic factors. Substitution of fresh water for salt and rise of the general land surface are essentially factors imposed upon the vegetation from outside and must be distinguished from factors operating within an autogenic sere.

It is true that the 'silting factor', operating on various aquatic and semi-aquatic vegetation, is largely independent of the activities of the plants themselves, and so is the time of exposure to the air which Dr Chapman and others have shown to be so important in determining the zoning of salt-marsh and of littoral marine vegetation. But these are factors operating *within the factor-complex that governs the autogenic seral development.* Only when silting (or peat formation) raises the soil surface permanently above the ground water-level does it result in that complete change of conditions which marks the passage from one formation to another and determines the appearance of a new set of life forms.

There remains the question of just how, on this basis, we should apply the term 'formation' to the actual plant communities involved—a question which, I fear, is not adequately dealt with in *The British Islands and their Vegetation*, though it was considered in a much earlier paper of mine (The classification of vegetation and the concept of development, *J. Ecol.* **8**, 1920, pp. 139–44). Clements regards the climax alone (which is of course restricted by him to the climatic climax) as the formation. But if we are to use his 'organism' idea at all, we should include developmental stages leading up to a climax as parts of the formation, since developmental stages are part of an organism. That was the view I took in 1920, and it was the extreme artificiality of considering plankton, for instance, as a developmental stage of, and therefore part of, the 'quasi-organism' whose adult form is climax forest that led me to break away from the pure Clementsian doctrine and to recognize that one formation is replaced by another very frequently in most priseres, thus extending the conception of climax to positions of equilibrium other than those determined by climate alone. Within each formation, on this view, there are developmental stages preceding the climax, an autogenic sere (or seres) within the influence of the dominating factor-complex which determines the formation. Thus I should regard the heath communities preceding Callunetum in succession as parts of the heath formation, and the ash-oak wood which was shown by Watt to precede the climax beech forest of the South Downs plateau as belonging to the same formation as the beech forest.

The effects of tidal salt water periodically flooding an area of salt marsh, though for very different periods at different levels, leads to zonal differentiation of the vegetation corresponding generally with increased height of the soil surface by silting. But the perpetual shifting of tidal currents and the formation of drainage channels leads to constant change of local conditions, great micro-physiographic complexity of the topography, and consequent instability of particular communities. Salt-marsh vegetation is, as Dr Chapman truly says, essentially 'dynamic'—very dynamic indeed! Under such conditions 'climax' communities—such as Juncetum maritimi—lose the preponderating position they hold in vegetation developed under more stable conditions in favour of the whole seral plexus. This is true of all 'migratory' formations in Crampton's phraseology, that is of all vegetation developed under conditions of intense physiographic dynamism.

On this view the whole of the halophytic vegetation of the salt marsh, from Salicornietum to Juncetum maritimi or Juncetum gerardii, belongs to the salt-marsh formation. Dr Chapman's diagrams of succession show that the seral relations are complex, but the whole plexus of communities is sharply defined from those outside it because of the decisive effect of the master factors. The moss or bog formation is another example of the same kind. On the other hand, there are many formations about whose limits there may well be differences of opinion, just as there are many genera of plants distinguished by some authorities and not by others. It can never be too strongly emphasized that the concept of 'formation', like the concept of 'genus', is part of a conceptual framework whose purpose is to correlate facts of nature in convenient and intelligible form. In my judgement this purpose is best served by the conception here adopted, which gives weight to the facts of succession, of positions of relative equilibrium, of life form, and of the determining master factors. The more detailed the study of a formation, of the changes within it, and of the changes which establish essentially different vegetation, the closer will be the fit of the conceptual framework to the facts.

NOTES ON VEGETATION CHANGES ON CAVENHAM HEATH, BRECKLAND

By E. PICKWORTH FARROW

(*With Plate* 5)

The two accompanying photographs will probably prove of considerable interest to readers of the *Journal of Ecology*, as they show more advanced stages in the vegetation of Breckland originally described in the *Journal* from 1915 onwards.

The first photograph is of great interest to me as I felt quite sure that the light sandy soil would suit *Pinus sylvestris* far better than *Betula alba*, and that the darker shade of the former would crowd out the latter. Experiment, however, has proved that quite the opposite is the case.

It may be remembered that small *Pinus* and *Betula* trees, about 30 cm. high, were planted in a large rabbit-proof experimental quadrat and on the exposed grass heath round about. Three trees inside the quadrat lived, but all the trees planted round about were killed by the rabbit attack. The original wooden stakes supporting the rabbit-proof wire netting decayed and were replaced by angle-iron stakes, which proved satisfactory, and are to be recommended for similar experimental quadrats.

The *Betula alba* trees are now well over 6 m. high, and it seems quite clear that the whole of these very dry East Anglian heaths (which it used to be supposed might be primitively treeless) would quickly become converted into quite dense woodlands if it were not for the rabbit attack, and other grazing influences, and for the effects of man. As mentioned in previous articles in this *Journal* it seems likely that this particular detrimental influence considerably affects the vegetation of much of the world where attack by animals upon the young trees and other plants is general or ubiquitous. Perhaps even parts of some arid regions were originally covered by plant life and would gradually become so again if animal 'pressure' were to cease.

The second photograph shows a large island of *Pteridium aquilinum* over 10 m. across on the middle of the extensive grass-heath association (degenerated *Calluna* heath) on Cavenham Heath a long way from a main bracken association. Anybody seeing this island for the first time might wonder how it came to be growing there, as there is no nearby association from which it could have spread by rhizome growth.

However, I noticed the establishment of this colony in the autumn of 1913—just a few fronds growing on the sides of a rabbit burrow as shown very prettily in phot. 7, Pl. 19, this *Journal*, **3**, 1915. Apparently the moisture conditions in this burrow were suitable for spore germination and prothallus production, although the surface of the grass-heath itself is far too dry for this to occur. The radius of the island is at present approximately 5 m. This gives a measure of the rate of rhizome growth of the *Pteridium* during the 28 intervening years, apparently only a little over 17 cm. a year in the very dry upper sandy layers of this Breckland Heath.

Phot. 1 *Betula alba* trees (somewhat less than 30 years old) completely overtopping and crowding out *Pinus sylvestris* in the large quadrat on Cavenham Heath. Two *Betula alba* trunks are seen on the left and a much thinner *Pinus sylvestris* trunk on the right. The latter tree has been completely overtopped and is being crowded out by the *Betula*. The *Pinus* foliage in the centre is darker than the other.

Phot 2. Large Island of *Pteridium aquilinum* spread originally from a prothallus established in a damp rabbit burrow on Cavenham Heath The very early stages of this were shown in this *Journal*, **3**, Pl. 19, phot. 7, 1915. The bracken has now spread by rhizome growth from the sides of the burrow forming a large island over 10 m across in the middle of the grass heath (degenerated from *Calluna* heath by rabbit attack) a long way from another bracken association.

STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

VIII. A SECOND SURVEY OF THE CHALK GRASSLANDS OF THE SOUTH DOWNS

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(*With Plates* 6–19, *containing phots.* 1–28, *and six Figures in the Text*)

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I. INTRODUCTION

In 1935 and 1936 a second survey was made of certain areas of chalk grassland originally examined by Tansley & Adamson in 1920 and 1921 (Tansley & Adamson, 1925, 1926; nos. III and IV of these 'Studies'). The purpose of the present paper is to compare the results of the recent survey with those of the original one. The grasslands examined are all natural, i.e. agriculturally untreated apart from grazing.

Two areas where successional change has been in progress were dealt with in a previous paper of this series (Hope-Simpson, 1940*b*). The present study deals with mature grasslands.[1] The changes observed in them are mostly to be regarded as non-successional fluctuations, although there are exceptions. Of these the most obvious is colonization by scrub; and the general spread of *Brachypodium pinnatum* which has taken place in the last 30 years or more (p. 252) cannot be considered a fluctuation in the same sense as the other changes observed in the herbaceous vegetation.

Apart from the hardly relevant case of short-term agricultural studies of grassland changes under experimentally altered management, knowledge of non-successional fluctuations is more advanced in the realm of animal than of plant ecology. This is natural because analogous fluctuations take place in a shorter time in many animal communities. The only botanical studies of the subject in the accessible literature are the very valuable ones made on the Park Grass plots at Rothamsted (see, e.g., Brenchley, 1935). The circumstances of the Rothamsted work differ in many ways from those of the present investigation, one of the chief differences being that there are no fluctuations of grazing on the Park Grass plots; but there is at least one feature of the results which is very relevant here. Changes, apparently spontaneous, in the proportions of single species or of groups of species (grasses, Leguminosae and other herbs) often show a periodicity in which a rise and fall are completed in about 5 years, correlation with the weather being obvious only in very abnormal years. It is very likely that more than one such cycle has been passed through on many of the South Down grasslands in the period of 15 years involved in the present study, and when reference is made to a particular change, or to the absence of change, after 15 years, it must always be remembered that more than one cycle of fluctuation may have occurred in the meantime.

Among incidental references to non-seral changes, that of Clements (1934) describes how in North America the short-grass plains of the middle-west revealed their potential 'mid-grass' character under the wet conditions about the year 1915; fluctuations have been noticed since that time. Relict areas protected from grazing showed a similar dominance of mid-grasses. Clements emphasizes the influence of climatic changes, and the value of studying changes in vegetation over intervals of 5 or 10 years.

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[1] Area 23 bears grassland which may be immature (see p. 243).

In 1920, detailed observations and lists were made by Tansley and Adamson on seventeen areas of chalk grassland[1] on the borders of Hampshire and Sussex (Tansley & Adamson, 1925, Studies III). Two of the areas had been under observation at intervals since 1908. The same workers extended their observations in 1921 by making notes and lists on forty-five more areas[2] in Sussex, between the Hampshire border and the eastern extremity of the South Downs at Beachy Head; these records were supplemented by Tansley and Gilbert-Carter in June, 1923 (Tansley & Adamson, 1926, Studies IV).

With the object of discovering what major changes, if any, had taken place, the writer undertook in 1935 and 1936, under Prof. Tansley's supervision, a second survey of as many of the total sixty-two areas as could be identified again with reasonable accuracy. At various times since 1936 a few further observations were made and doubtful points checked. The number of areas whose flora was listed a second time amounted to thirty-eight—eleven of those dealt with in Studies III, and twenty-seven of those added by Studies IV. Six other areas which were not identified closely enough to justify listing the flora were nevertheless recognized as being part of some particular expanse of grassland. In these cases notes were made about the general condition of the area as a whole in comparison with the records of the first survey. Changes in three other areas have been shown with photographs as the sole evidence (pp. 239–40). Altogether, therefore, forty-seven areas have been inspected in both of the surveys.

In all considerations of the surveys as wholes, the Hampshire border areas of Studies III, and the chalk grasslands and chalk heaths of Studies IV are treated as a single series.

II. METHODS

The areas were primarily identified in a traverse of the downs made in 1935 by Prof. Tansley and the writer. Since the first survey was undertaken solely with the object of collecting data from a representative range of chalk grasslands, and not with a view to any later visits being made, the areas were not marked as closely as would otherwise have been possible. Nevertheless, evidence of various kinds was available as to the identity of the area previously surveyed. Here it seems necessary only to state that all possible care was taken to locate the areas correctly and that doubtful cases were omitted from detailed study.

During the second survey evidence was collected for as many of the areas as possible about the recent operation of controlling factors. Naturally the main factor liable to change appreciably during the period involved is grazing.

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[1] Also two areas not strictly belonging to the chalk grassland association, which are not considered here; and two undergoing succession, which have already been dealt with (Hope-Simpson, 1940*b*).

[2] Also two more areas not strictly belonging to the chalk grassland association, which are not considered here.

Sometimes direct information was to be had from shepherds and others about the recent influence of grazing animals. More frequently the only evidence was in the vegetation itself. The notes given by Tansley & Adamson, particularly in Studies IV, generally describe the condition of the grassland and state the approximate depth of the herbage. In certain cases in the second survey there was a difference from the earlier description which indicated unmistakably an increase or a decrease in grazing. Of course it was not always possible to tell how long the new conditions had obtained, nor to be sure that they had not been preceded by a change in another direction. Similarly where no difference was manifest, there may have been changes in the intervening period.

THE METHOD OF RECORDING FREQUENCY

In both surveys, frequencies were estimated subjectively and recorded by the usual symbols, detailed elsewhere (Hope-Simpson, 1940*a*, p. 196), or by combinations of them.

It has unfortunately been necessary to deal at considerable length with the question of the errors involved in this method of recording frequency in order to reach some conclusion as to how the primary data are to be interpreted. Unless this question is thoroughly examined it is possible to arrive at a number of totally different results, some very far from the truth.

Tests of the subjective method as used by the writer

In a previous paper (1940*a*) tests are described in which lists were made more than once in the same area, under various circumstances; for instance, within a few days of each other, or at different seasons of the year, or at the same season in two successive years, or on two distinct parts of the same general area. This study resulted in a number of findings which must be used in comparing the data of the two surveys. Those most immediately applying are the following:

According to variations in the circumstances just mentioned, from 12 to 23% of the combined number of species listed on the two occasions disagreed as to assigned frequency by more than one unit, e.g. r. in one list, f. in the other, or absent in one list, o. l.f. in the other. A difference of more than one unit is shortly described as 'disagreement' of symbol. Differences smaller than this arise very commonly as errors, and the word 'disagreement' as used in this context does not include them.

The species subject to widest discrepancy purely by 'error' are mainly of the following three types:

(*a*) Grasses, other narrow-leaved plants and bryophytes (all difficult to observe).

(*b*) Annuals and biennials. These fluctuate greatly in abundance from year to year. Differences in the frequency of such species are not significant for the present purpose, which is to study changes connected with the lapse of a number of years.

(*c*) Species changing much in abundance of above-ground parts or in conspicuousness (e.g. flowering) throughout the season. These are a source of discrepancy between records made at different stages in the seasonal progress of the vegetation. In some species, for example those with conspicuous flowers and a short flowering period, quite a short interval at the relevant time of year may cause a considerable difference in recorded abundance.

Comparison of subjective estimations as used in the two surveys

The tests just alluded to do not furnish all the data needed for interpreting the results of the two surveys. Two further possibilities have to be considered:

(1) The range of error in the first survey may be different from the writer's as revealed in the tests just described.

(2) The frequency symbols may have had a different meaning attached to them in the two surveys, despite the writer's efforts to acquire the same standard from Prof. Tansley in the field in 1935.

Ranges of error of the two surveys compared.

It might be assumed that about the same range of error as applies to the writer's records would also apply to those of Tansley & Adamson. This supposition has been checked in the following way. On area HB 3,[1] specific frequency determinations (the percentage of occurrences of each species in fifty random casts of a 30 × 30 cm. frame) were made by Tansley & Adamson and also by the writer, in addition to the usual subjective estimations. The results are given in Table B (Appendix, p. 266). The specific frequency determinations are relatively objective. They are furthermore shown by the duplicate counts made in 1937 to be liable to much less error than attaches to the subjective estimates, even though the duplicate counts were made at different seasons—a fact responsible in some species for a considerable divergence between the two counts. The specific frequency figures may therefore be used as a relatively error-free standard of comparison. By comparing the subjective estimates of the different observers with their own specific frequency determinations made at the same season of the year, it is shown that the subjective estimates of both parties covered a similar range of error.

In addition to the check provided by these data from a particular area, a notion may be obtained of the respective thoroughness with which the two surveys were made by considering the average length of the lists obtained. It is of course assumed that over the whole set of areas there has been no real alteration in the average number of species per area. The average numbers of species recorded per area for twenty-eight Sussex Down areas are: first survey, 49; second survey, 47; and for eight Hampshire border areas: first survey, 39;

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[1] Explanation of reference numbers on p. 227.

second survey, 41. These figures show that the listing of the species followed about the same standard of detail in both surveys.

This is by no means a foregone conclusion. It was found (Hope-Simpson, 1940*a*) in testing the difference between normal and 'extra-careful' frequency estimation on area HB 18 that if one traversed the area over and over again in an attempt to evaluate the frequencies more truly, one inevitably continued to meet previously unobserved species; so that the list became one and a half times as long as the normal. Thus the similar average length of list over all the areas may be taken, in the absence of other evidence, as an indication that approximately the same care has been given in the two surveys to listing the species and assigning their frequencies, and that the error in the latter is of the same order.

Different values of symbols in the two surveys.

For area HB 3 the data in Table B (Appendix) make it possible to obtain numerical values in terms of mean specific frequency for various subjective symbols as used on the two occasions of survey. For instance, the specific frequency equivalent of 'abundant' is the mean of the specific frequency values of the species recorded as a. at the time of survey. These numerical values show that the mean specific frequencies of a., f., o., r. and l. differed considerably in the usage of the different investigators. The values are as follows (r. and l. treated together):

	Tansley & Adamson	Hope-Simpson
a.	82	74
f.	29	47
o.	11	16
r. + l.	0	8

It is seen that for a species to be described as 'abundant' it perhaps needed to be slightly more abundant in the original survey of the area than in the recent one, although the difference is scarcely significant. On the other hand, the terms f., o., r. and l. were given in 1920 to species less common than those recorded by the same terms in 1936.

Evidence of a different kind shows that substantially the same state of affairs is general for the areas dealt with in the South Down surveys. This may be seen by counting the number of times the symbols v.a., a., f., o., r. and l. were used in the first and in the second surveys of thirty areas. The symbols reach the following totals:

	First survey (Tansley & Adamson)		Second survey (Hope-Simpson)	
v.a.	35		32	
a.	170		184	
f.	280		145	
o.	429		212	
r.	83	208	474	554
l.	125		80	
Total	1122		1127	

Counts from eight Hampshire border areas totalled independently give a similar result. It is assumed that on as many as thirty areas there has been no real alteration in the total numbers of plants at the various levels of frequency. This being so, the striking point revealed is the very different use of the term 'rare', a difference which affects the use of the symbols o. and f.

Fig. 1 presents these numbers diagrammatically, placing them in sequence extending from the rare and local records to the very abundant. Curiously the counts given above reach almost the same total for the two surveys so that the numbers could be plotted direct. It should be noted that intermediate symbols, such as f.–a., or those prefixed by l., are not counted; and also that presentation of the numbers on a linear scale may give a somewhat distorted impression because the occurrences are in reality more densely massed at the abundant and especially the rare level than in between (cf. Raunkiaer, 1918). For these reasons Fig. 1 must not be interpreted too closely. It is nevertheless clear that the value of 'occasional' in the first survey is nearer to the 'rare' or 'local' than to the 'occasional' of the second survey.

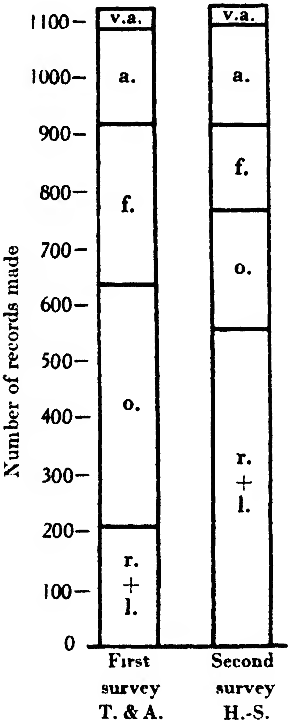


Fig. 1. Diagram showing the range of frequency covered by given symbols as used in the first and second surveys of thirty areas. Rectangles, whose height represents the number of times the symbol was used in the survey, are placed one above another in order of increasing frequency so that the total height of each column represents the total number of records made by all the symbols counted—1122 in the first survey, 1127 in the second. The totals for r. and l. have been added together since it is impossible to place them in order of frequency.

In comparing the original and the recent records, it has been difficult to make adequate allowance for the fact that 'occasional' and 'rare' signified a higher degree of frequency in the second survey. A consequence of this difficulty is that cases of genuine increase have frequently not been detected.

Thus decreases are mentioned a good deal more often than increases in the notes on specific changes given later (§ III).

Method of interpreting data

In deducing vegetational changes from the subjective frequency data obtained by the different workers, the procedure regularly adopted for each area has, in view of the findings just described, been guided by the following points, although a certain latitude in interpretation has been necessary according to matters of experience which cannot be mentioned individually.

(1) Of the species recorded from the area, the percentage which show disagreement is noted. Fig. 1 has been used as an aid to deciding whether a difference is equivalent to disagreement. It shows, for example, that although the symbols o. (first survey) and f. (second survey) are nominally only one unit apart, the difference between them amounts to disagreement, while between f. (first survey) and o. (second survey) it does not.

(2) Even differences amounting to disagreement are, however, by no means always significant (Hope-Simpson, 1940*a*). Depending mainly upon (*a*) whether the two surveys of the area were made in the same or in different seasons of the year, and (*b*) how closely the area was identified, a certain proportion of the cases of disagreement may be deemed to indicate a real change.

(3) To decide which species are most likely to contribute to this number, knowledge derived from the tests described in the previous paper (1940*a*), and from general experience in the field, is used. Matters considered are (*a*) the amount of discrepancy between the records, (*b*) the conspicuousness of the species, (*c*) its liability to fluctuate annually, or (*d*) seasonally.

By taking many precautions against concluding falsely that a change has taken place in the abundance of any species, cases are probably often missed where quite a large change has taken place. Indeed, this can be seen in the instance of Chalton Down quoted below (p. 225 and Table 2). Furthermore, a one-sided impression is gained of the species which have changed, because those which it is possible to detail are in the main those which do not have to be excluded as liable to error. The absence of reference to species whose frequency is estimated with difficulty, or which change greatly through the season, does not mean that they may not have undergone very significant changes in abundance since the first survey.

Tests of validity of deductions by the method adopted

Whether the method of interpretation adopted works out consistently can, up to a point, be tested.

For area HB 18 two recent lists made in the ordinary way are available (29 September 1936 and 26 July 1938). They have each been compared separately with the 1920 list in the manner adopted throughout the present study. The changes in abundance thus deduced as significant on the basis of (*a*) the 1936 list and (*b*) the 1938 list are shown in Table 1. Where marked ? under (*a*) or (*b*) the evidence is not considered good enough to make a definite statement as to change.

Table 1. *Duplicate examples of interpretation of data, area* HB 18

I = increase; D = decrease; ? = doubtful

Species	Changes deduced (*a*) 1920 and 1936 comparison	(*b*) 1920 and 1938 comparison	Correspondence between (*a*) and (*b*)
Hieracium pilosella	?	I	?
Bellis perennis	I	I	+
Plantago lanceolata	I	I	+
Dicranum scoparium	I	? (I suggested)	? +
Avena pubescens	D	D	+
Brachythecium purum	D	D	+
Neckera crispa	D	D	+
Cladonia fimbriata	D	D	+
Camptothecium lutescens	? (D suggested)	D	? +

The table reveals a satisfactory correspondence, the interpretation agreeing for six species and not conflicting for the other three, and thus indicates that some reliance can be placed upon the method of interpretation. It does not of course prove that the changes have really occurred, since there is no check on the accuracy of the single first survey list.

Fortunately, however, this last point can be tested for another area, that on Chalton Down, whence specific frequency results are available (p. 221). These make it possible to test the validity of conclusions as to change, based on the subjective frequency records, since we can compare the results arrived at by the two methods. Table B (Appendix) gives the primary data, and Table 2 (p. 226) shows how the deductions from subjective frequencies are substantiated by the specific frequencies. The 1937 figures used for the latter are those of September (corresponding with September 1920), not those of May. In the column showing changes indicated by the specific frequencies, the cases marked ? are considered doubtful because the differences between the figures given in the previous column are so small as to be possibly due only to errors, or, in the case of *Taraxacum* and *Briza media*, because the duplicate figures for 1937 show a wide error for these species.

From the subjective results only one species (*Dicranum scoparium*) can, according to the standard adopted throughout this work in deducing changes, be said to have altered in abundance. Its specific frequency figures support the conclusion exceptionally strongly. But Table 2 also gives, in column 3, the conclusions obtained by taking the differences in subjective frequencies at nearer their face value (after allowing for the different meaning of the symbols of 1920 and 1936). It reveals that more than half of the deductions by this 'looser standard' are substantiated by the specific frequency data, and the remainder are not contradicted. Indeed it might be thought reasonable to adopt this standard, until it is recalled that to do so would be at variance

Table 2. *Changes on area* HB 3 *concluded from subjective and from specific frequencies*

I = increase; D = decrease; ? = doubtful; . = no evidence

	1		2	3	4		5	6
	Subjective frequencies				Specific frequencies			
	Symbols		Change concluded by standard adopted	Change concluded by looser standard	Figures		Change indicated	Correspondence of changes concluded from subjective symbols (columns 2 and 3) with those from specific frequency figures (column 5)
Species	1920	1936			1920	1937		
Carex caryophyllea	o.	f.	.	I	22	38	I	+
Euphrasia nemorosa	o.	o.–l.a.	.	I	2	14	I	+
Poterium sanguisorba	o.–l.v.a.	v.a.	.	I	56	90	I	+
Galium verum	a.	l.	.	D	34	10	D	+
Leontodon autumnalis	o.	abs.	.	D	22	2	D	+
Pimpinella saxifraga	f.	r.	.	D	20	8	D	+
Dicranum scoparium	f.–a.	abs.	D	D	64	2	D	+ +
Bellis perennis	o.	abs.	.	D	6	2	?	? +
Daucus carota	o.	abs.	.	D	4	0	?	? +
Succisa pratensis	o.	abs.	.	D	2	0	?	? +
Taraxacum spp.	o.–f.	r.	.	D	14	4	?	? +
Campanula glomerata	o.	abs.	.	D	0	0	.	.
Briza media	f.	abs.*	.*	.*	42	60	?	.

* The failure to record *Briza media* in 1936 could, in view of its high constancy, be guessed as a complete oversight.

with the conclusions already reached from a wider study of the errors. The satisfactory result of the check on the looser standard is perhaps largely due to fortuitous accuracy in these particular subjective estimations, since the observer's accuracy doubtless varies from time to time. However, since approximately correct conclusions are in this case derived from an interpretation of subjective results a good deal less cautious than the standard decided upon, it may be concluded that the latter standard allows a good margin of safety against false deductions. On this basis the results of the two surveys have been considered area by area.

NOMENCLATURE

The nomenclature of the angiosperms is derived from the same sources as in Studies VI (Hope-Simpson, 1940*b*, p. 389), and of the cryptogams as in Studies VII (Hope-Simpson, 1941, p. 109).

Certain pairs or groups of allied species have usually been considered together, because it is impossible to rely on their separate recognition in the field on every occasion, for example in the absence of flowers or fruits, and difficult to estimate their frequencies independently in areas where they occur together. The species concerned are the following:

Agrostis spp. *A. stolonifera*, *A. tenuis* and related forms.

Festuca ovina+*rubra*. It is clear that *F. rubra* was commonly overlooked in the first survey. In most if not all cases, *F. rubra* occurs with *F. ovina*, in the form *genuina*, not *commutata* (*fallax*).

Galium erectum+*mollugo*. Nearly always the former.

Sonchus asper+*oleraceus*.

Taraxacum spp. Presumably always either *T. officinale* or *T. erythrospermum*. Plants in the vegetative state, with somewhat deeply cut leaves, were not certainly distinguished in the second survey as one species or the other.

Viola riviniana+*sylvestris*. Generally the former.

III. AREAS CONSIDERED INDIVIDUALLY

The areas numbered 3, 4, etc., in this paper and those lettered A, B and D (chalk heaths) have the same reference in Studies IV. Those numbered here as HB 3, HB 5, etc., are the areas of corresponding number (3, 5, etc.) in Studies III (Hampshire Border). 1 is the same area as HB 3, and 2 as HB 12. The areas will now be considered in numerical order (except HB 8 and HB 9), with the Hampshire Border series of Studies III preceding the Sussex Down series of Studies IV, i.e. approximately from west to east except for three chalk heaths, which are dealt with last. Areas HB 8 and HB 9, where experiments have been in operation, are treated first in greater detail than the other areas.

Owing to the data being more precise for some areas than for others, the results are very uneven in their degree of detail. More consideration is given, for instance, to minor features on the areas at Downley Bottom than to other grasslands where the dominants have changed over a wide expanse, although the latter changes are of greater importance.

As an index of floristic change, there is given for most of the areas the number of species held in common by the two lists, as a percentage of the number in the shorter list. The latter number affords a fairer basis for the percentage than the grand total of species for both lists, because the longer list may often be longer solely because more time was spent in making it, and not through any real difference in the flora (Hope-Simpson, 1940*a*).

HB 8 AND HB 9. DOWNLEY BOTTOM

The two areas HB 8 and HB 9 at Downley Bottom, on gently sloping rabbit-grazed grassland of westerly exposure, were the scene of experiments started by Tansley in 1908–9. Early in 1909 a wire fence, proof against rabbits and stock, was erected on each area so as to enclose a plot of grassland and the margin of the adjacent wood. The vegetation inside and outside the fences was observed at intervals until 1920. The results dealing with the woody plants appear in Studies II (Tansley, 1922) and with the herbaceous vegetation in Studies III.

The experiments had to be abandoned when there was a change in ownership of the estate in 1922. The fences were intact until this time, but were not maintained thereafter and consequently collapsed from natural causes. They are now non-existent except for some of the posts and buried wire. It may be surmised that rabbits made their way into the enclosures by about 1924. Although unfortunate from the standpoint of the original purposes of the experiments, this history does in fact reproduce under controlled and exaggerated conditions a sequence of events which often occurs, and several interesting points are brought to light by the records of 1936. The lists made at Downley Bottom in 1914, 1920 and 1936 are given in Table A (Appendix, p. 263).

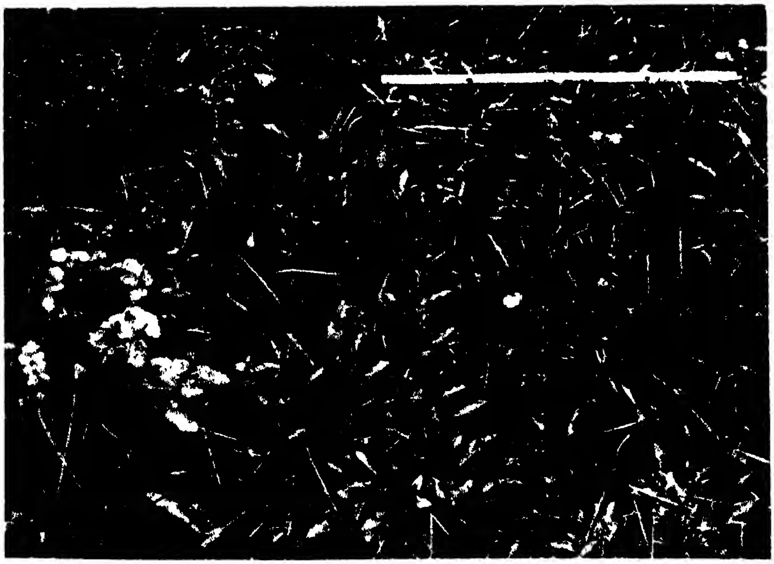
HB 8. *Downley Bottom, Area A*, 5 *October* 1936

North-west slope, 17–18°; grazed by cattle and rabbits. In 1919 a wooden fence was erected along the margin of the wood and passing round the enclosure outside the original fence (Phots. 1, 2). This does not prevent the entry of rabbits, although it may discourage them, but it forms a barrier to the cattle which graze the grassland outside. The differences now showing between the vegetation inside and outside the fence are therefore partly a legacy of the period of complete freedom from grazing inside, and partly a result of the difference in conditions since about 1924, i.e. grazing by cattle and rabbits outside, and by rabbits only inside. It appears that the differential grazing effects since 1924 (as between cattle plus rabbits and rabbits alone) have had the major influence, for the narrow belt of vegetation inside the wooden fence

Phot. 1. Downley Bottom, area A (HB 8). September 1911, about three years after erection of the wire fence. The difference inside was of course much greater when records were made in 1920, by which time many of the woody invaders seen in Phot. 2 had become established (cf. Tansley, 1922). The tall isolated plants are *Cirsium palustre*. (*J. Ecol.* **13**, Pl. III, phot. 1.)

Phot. 2. The same, 7 September 1937. The white stick marks the position of the corner post seen in Phot. 1. The tall stalks in the foreground belong to *Senecio jacobaea*. The large bushes seen in the enclosure are *Crataegus*.

Phot. 3. H B 8. Outside enclosure A, September 1920. Close to edge of wood. *Hylocomium splendens*, *H. squarrosum*, *Carex flacca*. The photograph covers rather more than 60 cm. from left to right. (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. V, phot. 3.)



Phot. 4. The same (site close to the last), 5 October 1936. Turf typical of that surrounding. *Pastinaca sativa*, *Leontodon hispidus*, *Carex flacca*, etc. Mosses less in evidence than in Phot. 3. Scale as Phot. 3; rule 30 cm. long.

Phot. 5. HB 8. Inside enclosure A, 5 October 1936. *Cirsium palustre*, *Clinopodium vulgare*, *Pastinaca sativa*, *Fragaria vesca*, etc. Scale as Phots. 3 and 4.

Phot. 6. War Down, west slope (HB 13), 29 August 1936. After about four years' complete absence of grazing. Herbage 10–25 cm. deep with tall inflorescences. *Leontodon hispidus* in flower and fruit, *Scabiosa columbaria* in flower. The planted trees visible are alders. The base of the spade, which is nearly 1 m. high, is at soil level.

but outside the derelict wire fence is very similar in appearance to that inside both fences, but markedly distinct from the much smoother turf outside both fences.

The extent of burial of the fallen wire netting is interesting. Parts of it which must have fallen to the ground at some time since 1924 are now below the turf but level with the soil surface, while in two spots measured (clear of the fringe of netting purposely buried in erecting the fence) it was covered by 3 cm. thickness of soil in addition to the thickness of the turf. This gives some notion of the rate at which soil movement is proceeding, under the influence of humus accumulation and turning of soil by rabbits, moles, ants and earthworms.

Changes outside enclosure A.

The population of rabbits is[1] about the same as it was in 1920, according to information given locally, and the depth of the turf (4–8 cm.) is the same. Cattle, which had been on the area for about 4 years prior to 1920, have pastured it regularly since then, especially in autumn and early winter. Soil has been exposed locally by rabbits and moles.

Species in common in 1920 and 1936 were 83 % of the shorter list, i.e. the flora is essentially unaltered.

The most obvious change has been an increase of casual and wood-edge plants, ascribable largely to their concentration within the enclosure whence they have spread.

Species decreased since 1920: *Viola riviniana + sylvestris*; probably also *Carex flacca*. Species increased: *Clinopodium vulgare*, *Leontodon hispidus*, *Pastinaca sativa*; probably also *Briza media*, *Crepis capillaris*. Phots. 3 and 4, of representative pieces of turf, confirm the greater quantity of *Carex flacca* in 1920 and of *Leontodon hispidus* and *Pastinaca sativa* in 1936.

The spread of *Pastinaca sativa*, now abundant and widely dispersed outside as well as inside the enclosure, is an interesting occurrence, because a note made by Tansley & Adamson shows how this began. It was absent in 1914 and appeared round holes dug in 1919 in the erection of the wooden fence. Doubtless the new establishment of a species often comes about through some such accident enabling it to occupy a centre whence it sheds an abundant supply of seed.

Crepis capillaris appears to have spread over Downley Bottom at large. It is absent from all the 1914 and 1920 records but now occurs outside and inside A and B enclosures.

Changes inside enclosure A.

Apart from the entry of rabbits, the chief factor causing change in the herbage since 1920 has been the growing influence of the scrub of *Crataegus*

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[1] Throughout this paper the present tense is used, for the sake of brevity and clearness, to refer to the time of the second survey (generally 1935–6), in contrast to the time of the first survey. does not refer, necessarily, to the date of publication.

and *Rosa* (Phot. 2). These are the survivors of the woody colonization described by Tansley (1922). A few smaller specimens are dead.

In 1920 the herbage was 15–30 cm. deep. It is now 4–10 cm. Inflorescences of *Pastinaca sativa* occur abundantly.

The number of species common to the 1920 and 1936 lists is 91 % of the shorter (1936) list. The floristic content thus differs mainly by the loss of species (55—46) rather than by their replacement by others.

The only specific changes of which the data give adequate evidence are the following: Probably decreased: *Avena pratensis*, *Galium erectum + mollugo*, *Brachythecium purum*; certainly increased: *Clinopodium vulgare*, *Pastinaca sativa*. The origin of the successful invasion of *Pastinaca* has already been noticed. There is no doubt that many species besides those mentioned have changed in abundance, and that in many cases there has been a change in the disposition of the plants even where the abundance remains about the same.

Comparison of herbage outside and inside enclosure A in 1936.

The differences showing in 1936 between the herbage outside and inside the enclosure are mainly due to the influence of the shrubs and the lighter grazing inside—what grazing there is inside being due to rabbits alone without the cattle which operate outside.

Depth of herbage, 1936: outside, av. 4–8 cm., slightly tussocky; inside, av. 4–10 cm., more tussocky than outside, the tussocks being mainly composed of *Poterium sanguisorba*.

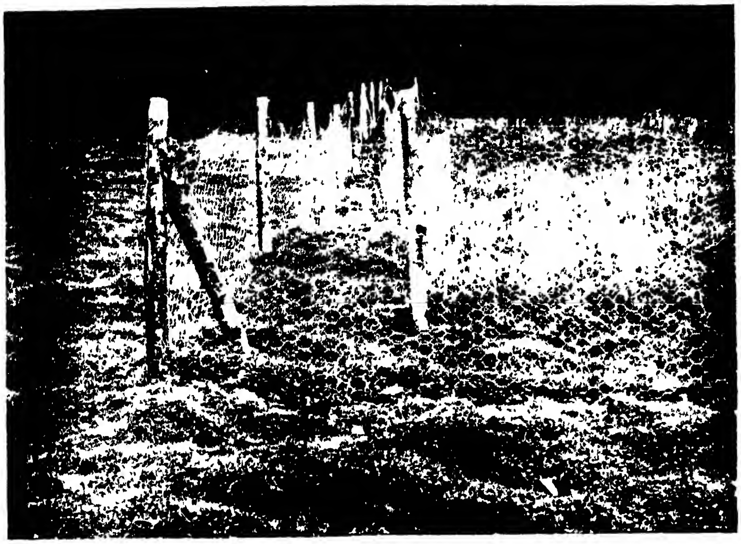
Specific differences: More abundant outside: *Euphrasia nemorosa*, *Trifolium repens*; more abundant inside: *Fragaria vesca*, *Scabiosa columbaria*.

Trifolium repens was found outside but not inside in 1914, 1920 and 1936, reflecting the long continued state of undergrazing inside the enclosure.

The existing differences are of course much greater than indicated merely by the depth of turf and the few specific differences which can be mentioned outside the limits of the errors involved in recording. The turf inside exhibits the lack of compactness characteristic of lightly grazed sites among scrub. Phots. 4 and 5 show the differences clearly, especially the greater preponderance inside of wood-edge and casual dicotyledons such as *Clinopodium vulgare*, a difference not indicated beyond doubt by the frequency records except in the case of *Fragaria vesca*.

HB 9. *Downley Bottom, Area B, 7 October* 1936

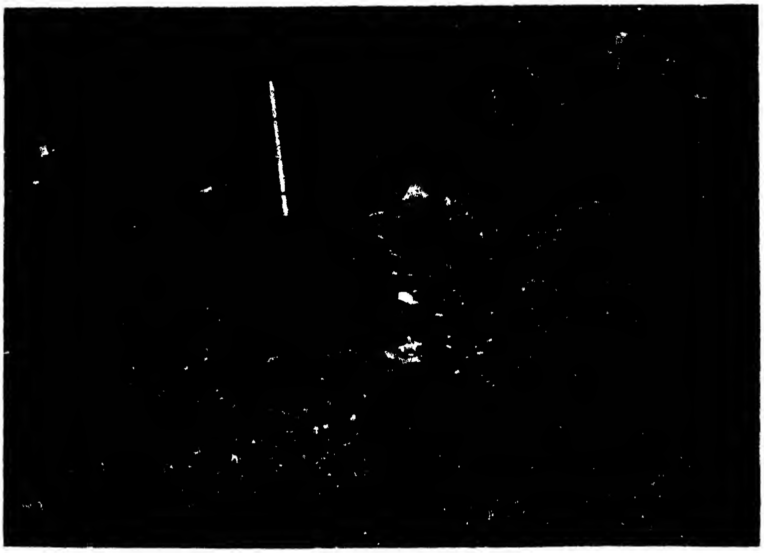
West slope 15–23°. Surface soil poor in carbonate (*p*H 7) though chalk lumps occur at 18 cm. depth. Heavily grazed by rabbits. The history of this area since 1920 is simpler than that of HB 8. Cattle are absent, and no wooden fence has been erected round the original enclosure (Phot. 8).



Phot. 7. Downley Bottom, area B (H B 9). September 1912, about 4 years after erection of the inner fence. The difference inside was much greater when records were made in 1920. (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. III, phot. 2.)

Phot. 8. The same, 5 October 1936, about 12 years after collapse of wire fence. The hawthorn bush conspicuous in Phot. 7 is now in the wood margin. The clump of *Rubus leucostachys* behind the fence on the extreme right survives from the mass developed during the period of enclosure (Tansley, 1922). Dead *Rosa* stem in front of third post from right.

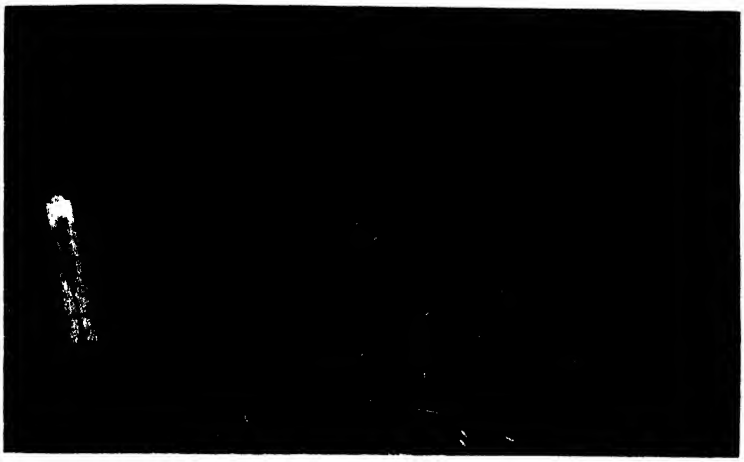
Phot. 9. HB 9, outside enclosure B. September 1914. Hummocky ground dominated by *Helianthemum nummularium* (flowering). The rule is 30 cm high from its base on the soil. (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. IV, phot. 3.)



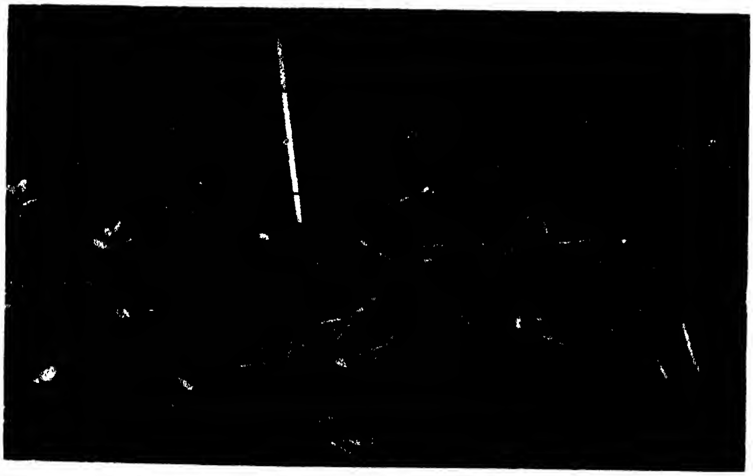
Phot. 10. The same, 5 October 1936. Ground still hummocky and dominated by *Helianthemum*. Scale as foreground of Phot. 9; rule 30 cm. high.

Phot. 11 HB 9, inside enclosure B, September 1914. *Holcus lanatus* left and centre, *Galium verum* centre and right, *Poterium sanguisorba*, etc. (Phot. A. G. Tansley *J. Ecol.* **13**, Pl. IV, Phot. 1.)

Phot. 12. The same, 5 October 1936. *Festuca ovina + rubra*, *Helianthemum nummularium* *Cirsium palustre*, *Senecio jacobaea*, etc. Scale as Phot. 11.



Phot. 13. H B 9, inside enclosure B, September 1914. *Calluna vulgaris* (flowering) centre, *Galium verum*, *Avena pratensis*, *Poterium sanguisorba*, etc. (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. IV, Phot. 2.)



Phot. 14. The same piece of ground as in Phot. 13, though not necessarily regarded from the same direction, 7 October 1936. Dead branches of *Calluna* right, dead *Senecio jacobaea* stalks standing on extreme right, *Myosotis arvensis* left, *Helianthemum nummularium*, etc. Exposed soil in centre. Scale as Phot. 13.

Phot. 15. HB 9, 7 September 1937. The tall stalks are *Cirsium palustre*, growing thickly inside the enclosure. Cf. Phot. 8, taken a year earlier.

Phot. 16. HB 9, 7 September 1937. View of enclosure from the south side. Tall stalks of *Cirsium palustre* visible against the wooden railings.

Changes outside enclosure B.

The rabbit population has not altered greatly since 1920, and the general appearance of the turf is the same (Phots. 7–10). But the depth of herbage was apparently rather greater in 1920 (4–9 cm.) than in 1936 (3–4 cm.).

The proportion of species in common is rather low, 66% of the shorter list. There is no obvious explanation.

There have been several changes in frequency of individual species. Species decreased: *Avena pratensis*, *Carex flacca*, *Cirsium acaule*,[1] *C. palustre*,[1] *Poterium sanguisorba*, *Trifolium pratense*; probably also *Hylocomium triquetrum*. Species increased: *Crepis capillaris*; probably also *Briza media*.

The changes in *Carex flacca*, *Crepis capillaris* and *Briza media* correspond with similar ones outside enclosure A. Since areas A and B are several hundred yards apart and have recently been under somewhat different grazing conditions, the causal influence is likely to be a widespread one such as weather, rather than a locally varying factor like grazing.

Changes inside enclosure B.

'Inside enclosure B' means within the remnants of the inner of the two wire fences, the outer of which was added as an additional protection.

The profound change in the appearance of the herbage as a result of renewed grazing is shown by Phots. 11–14. Its depth, which was 20–25 cm. in 1920, is now the same as outside the enclosure (3–4 cm.).

Species in common, 1920 and 1936—72% of shorter list. The present flora differs from that of 1920 mainly through the loss of species, whose number increased considerably between 1914 and 1920. Numbers of species (trees and shrubs omitted): 1914, 49; 1920, 64; 1936, 46.

The following are the well-attested specific changes: Species decreased: *Calluna vulgaris*, *Cirsium acaule*,[1] *Galium verum*; probably also *Poterium sanguisorba*, *Hylocomium triquetrum*; species increased: *Agrostis* spp., *Cirsium palustre*,[1] *Luzula campestris*.

These changes largely constitute a reversal of those which took place after the exclusion of rabbits, although this is not true of *Cirsium acaule*[1], and in the case of *Galium verum* and *Luzula* there is no clear evidence to this effect. The dead remains of *Calluna* are still visible in one place (Phot. 14, cf. Phot. 13). Of the other woody invaders away from the wood margin, plotted by Tansley (1922), one dead stem of *Rosa* sp. (Phot. 8) is the only remaining trace.

Comparison of herbage outside and inside enclosure B in 1936.

There is no difference obvious to the eye except that the turf is more broken by rabbit-scratching inside than outside. By comparing weight together with depth of the herbage outside the enclosure with the same values inside, Tansley & Adamson demonstrated quantitatively what is visible to the eye—

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[1] See below (p. 232).

the great reduction in the density of the herbage at ground level resulting from the withdrawal of grazing. It appears that the turf inside the fence has not yet fully recovered its typical compactness; the suddenness of the onslaught of grazing when the fence ceased to be a barrier to rabbits probably made such a recovery difficult.

A comparison of the lists made outside and inside the enclosure in 1936 shows no existing differences in occurrence or frequency of species greater than may arise through error. Other evidence is, however, available for the two thistles, *Cirsium acaule* and *C. palustre*. They were counted by Tansley & Adamson in 20 quadrats of ¼ sq. m. placed at random inside and outside the enclosure. They were sampled in the same way in 1936, and again outside the enclosure to test the sampling error, in May and September 1937. The results are shown in Fig. 2.

C. acaule has decreased greatly outside and inside the enclosure, presumably due to some common cause, but it is still distinctly rarer inside; in 1936 one plant occurred in twenty quarter-metre squares, as against twenty-seven in the same area outside the enclosure.

C. palustre has also decreased outside, but inside it has increased, not only so as to reach parity with its position in the continuously grazed herbage outside, but in excess of this amount so that it is now more abundant inside (twenty-one plants counted) than outside (thirteen counted). There seems little reason to doubt that the divergence is connected with the different treatment from 1909–24. On *a priori* grounds it would appear surprising that, accompanying this encouragement of *C. palustre* by the onset of grazing, there has been no corresponding encouragement of *C. acaule*, for the permanent rosette habit of the latter might be thought a better adaptation to grazing than are the tall leafy stems of *C. palustre*. It may, however, be observed in Fig. 2 that the decrease of *C. acaule* outside the enclosure is a good deal steeper than that of *C. palustre*, and it is possible that in the former species the factor or factors causing this decrease have been so influential as to override any effect of differential grazing.

The greater abundance of *C. palustre* inside the enclosure was not noticeable from a distance in October 1936 (Phot. 8), but in September 1937 a mass of tall stalks existed inside while they only occurred sparsely outside (Phots. 15, 16). All the plants grown up in 1937 would have been at the rosette stage in 1936, *C. palustre* being a biennial.

Downley Bottom—Conclusions

The recent changes on area B (HB 9) are more instructive than those on A (HB 8), because of the simpler course of events. Outside the enclosure the vegetation is essentially the same as in 1920 although there has been a number of changes in frequency. The general features of the herbage, as we have noted, were by 1936 the same inside the enclosure as outside, but in the case of the two thistles, for which fairly precise data are available, considerable differences still exist. In the one (*C. acaule*), the difference in frequency caused by exclusion of rabbits has been approximately maintained; in the other (*C. palustre*) the present difference reverses that caused by excluding the rabbits.

These facts about the two thistles exemplify clearly how the ecologist needs to be on his guard in attempting to interpret differences which he may record in grassland. If we did not know the history of enclosure B, and man-made clues such as the remains of the fences were removed, an explanation by existing factors of the different frequency of the thistles on part of area B would, if forthcoming at all, probably be mistaken or at best a half-truth.

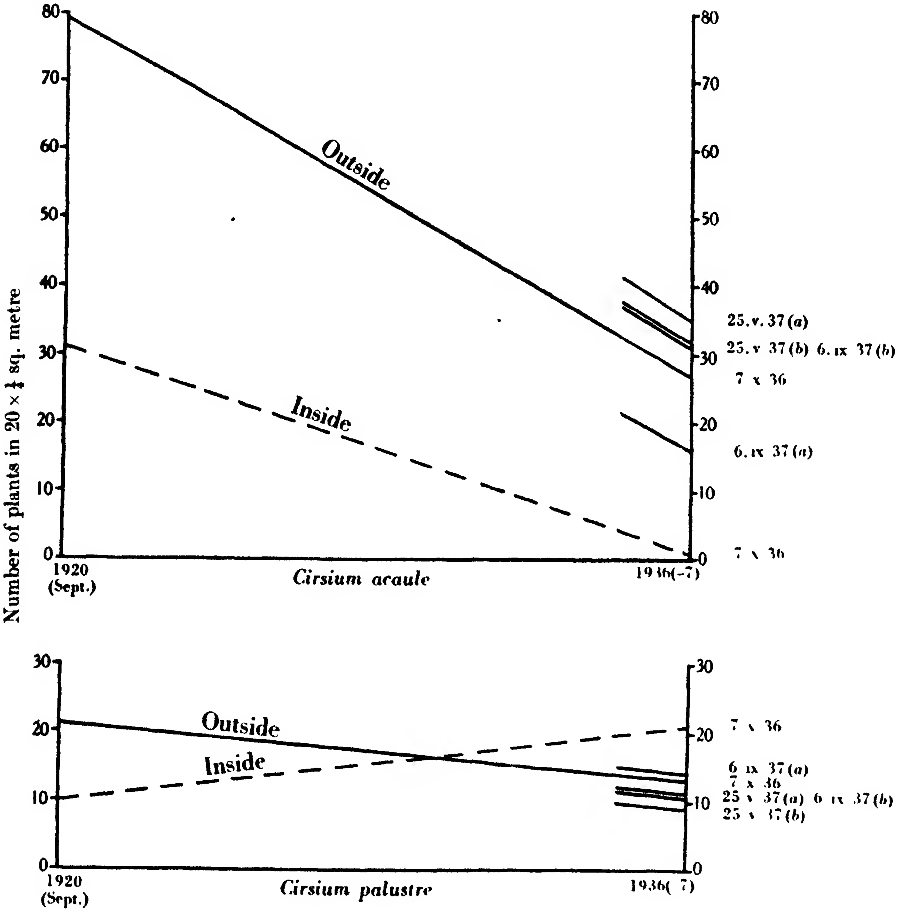

Fig. 2. Number of plants of *Cirsium acaule* and *C. palustre* in 20 quadrats of ¼ sq. m. cast at random outside and inside the enclosure on area HB 9, in 1920 and 1936(–7). On each of the dates shown by short lines (25 May 1937 and 6 September 1937) two additional counts (*a* and *b*) of each species were made outside as a test of error.

The general similarity to the outside turf which that inside has acquired since about 1924 shows that under conditions like those at Downley Bottom heavy grazing can, in a period of about 12 years, largely obliterate the effects of a previous 15-year period of complete freedom from grazing. Changes due to alteration, within certain limits, of grazing pressure are probably more readily reversible than most kinds of vegetational change, although severe over- or under-grazing frequently sets in train events which cannot subsequently be reversed by the grazing factor.

FORTY-FIVE OTHER AREAS

Of the following notes on these areas, some, printed in normal type, relate to areas which individually contribute interesting information. Others, in small type, are included to make the record complete and because they too are the source of data analysed in the next section of the paper (Section IV, p. 249).

HB 3 (=1). *Chalton Down, east slope,* 25 *August* 1936 *and* 8 *September* 1937

Identification certain although boundaries not so. Slope 24–32°. Juniper scrub. Grazed by sheep in 1920, rabbits in 1936–7. There is now no evidence of the grazing of sheep mentioned in Studies III and IV; instead there has been an increase of rabbit pressure. The turf appears to be rather shorter than in 1920 and a good deal more broken. The conditions for the grassland have been materially altered by the growth of the shrubs (Phots. 17, 18), which shelter the ground from wind, quite apart from the effect they have on the herbage within their individual areas of influence, which were avoided in making the list.

The second survey list is compared with that given in Studies IV; the one in III includes marginal plants.

Species in common, 1920 and 1936—85% of shorter list.

For this area we have much more reliable evidence than usual about changes in abundance, because specific frequency determinations are available (p. 221 and Table B, Appendix). Differences in the figures for 1920 and 1937 greater than are likely to be due to error[1] indicate the following changes. The figures give the specific frequencies (per cent) of September 1920 and September 1937, and the percentage decrease or increase:

Decrease				Increase			
	1920	1937	Difference		1920	1937	Difference
Avena pratensis	84	60	24	Achillea millefolium	8	22	14
A. pubescens	74	24	50	Agrostis spp.	4	38	34
Cirsium acaule	98	74	24	Campanula rotundifolia	32	74	42
Galium verum	34	10	24	Carex caryophyllea	22	38	16
Hieracium pilosella	94	70	24	Euphrasia nemorosa*	2	14	12
Leontodon autumnalis	22	2	20	Gentiana axillaris*	0	16	16
L. hispidus	100	76	24	Koeleria cristata	2	88	86
Linum catharticum*	82	36	46	Medicago lupulina	4	48	44
Lotus corniculatus	98	80	18	Polygala vulgaris	4	22	18
Pimpinella saxifraga	20	8	12	Poterium sanguisorba	56	90	34
Scabiosa columbaria	78	56	22	Prunella vulgaris	16	32	16
Dicranum scoparium	64	2	62	Trifolium pratense	14	64	50
Hylocomium triquetrum	48	16	32	Hypnum molluscum	0	16	16

* Annual or biennial, i.e. probably not a long-period change.

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[1] Some idea of the error in the specific frequency determinations for each species is derived by comparing the two sets of figures obtained in 1937 (Table B, Appendix).

Phot. 17. Chalton Down, east slope (HB 3, −1). April 1921. (Phot. A. G. Tansley, *J. Ecol.* **13**, Pl. 11, phot. 1.)

Phot. 18. The same, 3 October 1936. Grassland very similar in appearance to the 1921 condition but surface broken here and there by rabbits. The amount of growth made by the juniper bushes in 16 years is clearly shown.

Considering the inconsistency, in certain species, of duplicate specific frequency figures of the same year (Table B, Appendix), and also taking into account the special importance of species with a high frequency in one survey or the other, we may note as the more important changes the decreases in *Cirsium acaule*, *Leontodon hispidus* and *Dicranum scoparium* and the increase of *Trifolium pratense* and *Poterium sanguisorba*. The latter is often abundant in chalk grassland closely dotted with well-grown shrubs, a condition to which the Chalton Down area has recently attained.

In 1920 the 1 ft. square (30 × 30 cm.) quadrats contained an average of 16–17 species; the corresponding figures of 25 May 1937 and 8 September 1937 (calculated regarding *Festuca rubra* as synonymous with *F. ovina*) were 19·7 and 19·1 respectively. If the difference between 1920 and 1937 is outside the limits of error, it furnishes an instance of the effect which heavier, but not excessive, grazing has in increasing the number of species per small unit area.

HB 5. *Chalton Peak*, *east slope*, 28 *September* 1936

Identified fairly closely. Slope *c.* 20°. Open hawthorn scrub, much *Poterium* in the herbage, which was lightly grazed by sheep in 1920, and now is moderately heavily grazed by rabbits. It is evident from the description given by Adamson (1922, p. 209) that there has been a considerable increase of grazing pressure.

Species in common, 1920 and 1936—75 % of shorter list.

The preponderance of *Poterium sanguisorba* remains as before. Decrease in *Hieracium pilosella* and *Thymus serpyllum*, increase in *Viola hirta*.

HB 6. '*Herbland*', 27 *September* 1936

The identification is almost certain. Exposure east-north-east, slope irregular, average *c.* 20°. Bounded by beechwood on the west, with outlying patches of scrub. Herbage very mixed with many dicotyledons. The grazing, due to rabbits, is not heavy. Although the evidence from local inhabitants is conflicting, it is probable that the area bore woodland which was cleared some considerable time before the first survey.

Species in common, 1920 and 1936—82 % of shorter list.

Avena pubescens, *Carex flacca*, the fine-leaved fescues and *Lotus corniculatus* have all increased in abundance. These increases in constant species of mature chalk grassland would be expected in vegetation representing a late stage in colonization under grazing of a deforested area.

The following five areas (HB 10 and HB 12–HB 15) situated on War Down are now all part of a plantation made by the Forestry Commission (who kindly gave the writer access to the ground) and have the same recent history. About 1910 War Down was grazed by sheep and much of it was also very heavily populated with rabbits; local men recollect particularly the devastation of the north slope (HB 10) and the top (HB 14 and HB 15). At the time of the first survey (1920) there had been a considerable recovery from this state of affairs, except on the north slope where the rabbits still grazed heavily. This condition held until the summer of 1932, when the whole of War Down and the adjoining Holt Down were fenced with wire netting and the rabbits exterminated. Trees were planted at distances of 9 ft. (2·7 m.), but up to the present they leave the grassland virtually unaffected (see Phots. 19 and 20, of Holt Down).

HB 10. *War Down, north slope*, 27 *August* 1936

There is no doubt as to the correct location of the area. Escarpment slope 24–34°. In 1920 heavily grazed by rabbits with mosses conspicuous; in 1936 ungrazed and bearing long grass. The four years of enclosure preceding the second survey have produced a condition in area HB 10 very different from that described in Studies III, p. 208. The herbage averages 20–30 cm. deep, as against 7·5–10 cm. in 1920, and inflorescences are about 40–60 cm. tall. Grasses, notably *Festuca rubra*, are now overwhelmingly dominant (cf. 1920, 'The grasses particularly fall far behind their usual position in chalk grassland'). The mosses, which in 1920 were dominant in places, are still very abundant, practically forming a lower layer in the thick herbage. Only eight bryophyte species, however, were found in 1936 instead of the fifteen of 1920—almost certainly a significant difference. The rabbit warrens are rapidly becoming covered over by non-grassland species such as *Solanum dulcamara*, *Urtica dioica*, *Cirsium arvense* and *Epilobium angustifolium*, as well as by *Festuca rubra* and *Dactylis glomerata* which belong to the grassland itself.

Species in common, 1920 and 1936—69% of shorter list.

As regards specific changes, there have been increases of *Anthoxanthum odoratum*, *Carex caryophyllea*, *Festuca ovina + rubra*, *Taraxacum officinale* and *Trisetum flavescens*; and decreases of *Thymus serpyllum*, *Dicranum scoparium* and *Hylocomium squarrosum*. Out of nineteen species which show 'disagreement' of symbol (i.e. *wide* divergence, see p. 220) in the two lists, seven are mosses, and all of these have the lower recorded frequency in the second survey list.

HB 12 (=2). *War Down, east slope*, 26 *August* 1936

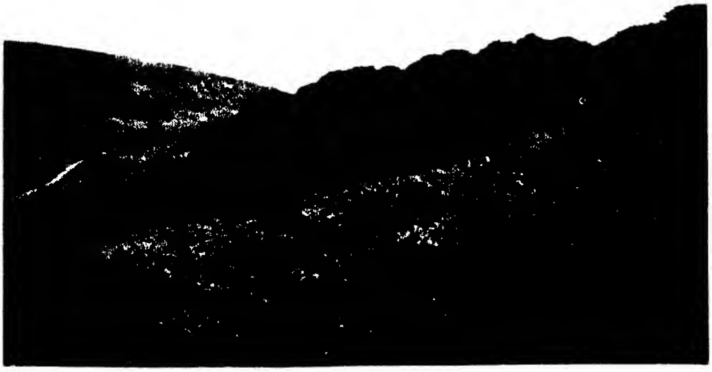
The area was identified fairly closely. Slope 16°. Pastured in 1920, ungrazed in 1936. The history of the area is stated above (p. 235). Again there has been a marked alteration in the grassland. The herbage, 7·5–10 cm. deep in 1920, now averages about 20 cm. although it varies considerably in thickness (10–30 cm.) in different parts of the area, revealing local differences in the habitat whose existence would not have been obvious when the turf was grazed to a common level.

Again the bryophyte flora has been much diminished, judging by the reduction of species in the list from sixteen to six.

Species in common, 1920 and 1936—60% of shorter list, a low value suggesting a rather large floristic change.

Decrease in *Cynosurus cristatus*, *Leontodon autumnalis*, *Prunella vulgaris*, *Trifolium repens*. Increase in *Avena pratensis* and *Brachypodium pinnatum*. The latter grass has newly appeared. The occurrence deserves comment on account of the ability of *Brachypodium pinnatum* to assume widespread dominance and so become something of an economic catastrophe to the farmer who uses the downs for grazing. The patch on area HB 12 is about 2 m. in

Phot. 19. Holt Down, west slope, about 1908 Closely rabbit-eaten turf with isolated hawthorns in the foreground, yew and beech behind. Slope of War Down, much bared by rabbits, on the left. Prior to enclosure by the Forestry Commission in 1932. War Down and Holt Down were, as wholes, under the same grazing conditions. (Phot. W. M Rankin *Types of British Vegetation* (ed. A. G. Tansley), Pl. XVIII*b*.)



Phot. 20. The same, 4 June 1940. The rabbit population was completely destroyed in 1932 Development of long grass, as shown in the foreground, has occurred to a similar extent on War Down, part of which is seen on the left. Planted beech and larch in the foreground.

diameter, and if there had been any quantity approaching this in 1920 it would with little doubt have been found in the 'thorough and persistent' search made by Tansley & Adamson (Studies III). It seems very probable that its establishment and spread has only become possible on this area with the cessation of grazing, although the plant might have been present in a suppressed state prior to 1932. The chalk grasslands in the Hampshire border district are almost all heavily grazed, with the recent exception of the new forestry enclosure, and *Brachypodium pinnatum* has not previously been found except as a very small patch (1·5 m. diam.) on Butser Hill, immediately west of War Down. Its occurrence on the chalk is spasmodic, and the nearest place where the writer has knowledge of its presence is on Duncton Down, 14 miles (23 km.) east of War Down; the quantity is small, and no larger amounts have been seen west of Steyning Round Hill, 27 miles (43 km.) from War Down.

HB 13. *War Down, west slope*, 29 *August* 1936

The area covered by the second survey may not have coincided with much of that of the first, but the grassland on the long western slope of War Down is uniform in type so that exact identification is probably unimportant (Phot. 6). Slope 19°. Now ungrazed. History, see p. 235. The herbage in most places is between 10 and 25 cm. deep. There are patches where the removal of rabbits has resulted in less marked growth than usual; *Cirsium acaule* is specially noticeable in these patches, as is also the case on the east side of the down (HB 12).

Species in common, 1920 and 1936—71 % of shorter list.

Decrease in *Plantago lanceolata*. Increase in the fine-leaved fescues, *Lotus corniculatus* and *Scabiosa columbaria*.

That exposure to the prevailing wind has an important determining effect on the herbage, at any rate when it is not grazed, is shown on the lee side (north-east) of the large clumps of bushes. In this direction from each clump there is an expanse of grass with unusually thick and deep green growth of the fescues. The effect extends well beyond the shaded zone and can scarcely be due to anything but shelter from wind.

HB 14. *War Down, summit, north end*, 29 *August* 1936

Flat top of the down. Surface soil neutral or slightly acid, though chalk lumps occur at 10 cm. depth. Now ungrazed. The area, whose history is given on p. 235, was not identified closely enough to justify making a list. It was expected that the local abundance of *Rhacomitrium lanuginosum* mentioned in Studies III would act as an indication of the site. After a widespread search only a small quantity of this moss was found; it seems certain that it has decreased greatly. Nor was it found again on areas HB 10 and HB 12 although a special watch was kept for it. Probably it has been smothered by the recently increased thickness of grass.

The present vegetation on the north end of the summit of War Down corresponds closely with the list made in 1920, but *Calluna vulgaris* has now appeared (locally frequent) and according to a local forester is spreading, an occurrence in accordance with the usual reaction of *Calluna* to decreased grazing. This area and the following one, lacking carbonate in the surface soil and bearing *Calluna*, may properly be classed as chalk heaths (p. 248).

HB 15. *War Down, summit, south end,* 7 *September* 1936

Located moderately closely. General character as HB 14. History, see p. 235. The herbage, which in 1920 was subject to fairly persistent rabbit nibbling, now averages 18 cm. in depth, with inflorescences 35–40 cm. high.

Species in common—70% of shorter list.

Calluna remains abundant as before. *Leontodon autumnalis* has decreased in abundance and *Poterium sanguisorba* has increased. The latter change appears to be typical of most parts of War Down since its enclosure in 1932. The species is by no means widespread on the down, but groups of large plants growing near together occur not infrequently and seem to be flourishing. It is the opinion of Mr S. E. Phelps, the local officer of the Forestry Commission, that after the elimination of rabbits *Poterium* became initially more conspicuous, but that its advance is now checked by the very thick mat of grass.

The changes in the War Down areas since 1920 have certainly resulted mainly from the four years of enclosure from 1932 to 1936. As would be expected, the result of excluding grazing is more pronounced on areas HB 10 and HB 12 (north and east aspect), which are sheltered from the prevailing winds and sun and consequently moist, than on HB 13 and HB 15 (west and plateau), which are more exposed to drying influences. Significant changes in frequency are adduced for eight and seven species respectively in areas HB 10 (north) and HB 12 (east), and for only four and two respectively in HB 13 (west) and HB 15 (plateau). The greater number of specific changes on the north and east exposures may be partly accounted for by the total flora being more numerous than on the other two areas, but is unlikely to be due entirely to this cause.

The influence of soil moisture upon the response of the turf to the withdrawal of grazing is clearly demonstrated by a trench and bank at the north-east point of the War Down afforestation enclosure. The bank, whatever its origin may have been, bears old and thoroughly mature grassland. The top and the rather steep slope facing the sun present a striking contrast to the thick surrounding growth. The turf is short and has much the appearance of turf in a similar situation not protected from grazing, such as is commonly encountered on the downs. This lack of growth after four years of enclosure at any rate shows that protection from grazing has a much slower effect in dry than in damp situations (cf. Farrow, 1925, Chap. 4).

HB 16. *Butser Hill (Ramsdean Down), north slope,*
29 *September* 1936

Identified fairly closely. Escarpment slope 25°. Now heavily grazed by rabbits. There is no external evidence available as to change in local factors or in the general character of the grassland.

Species in common, 1920 and 1936—65% of shorter list.

There has been an increase of *Holcus lanatus*. *Arrhenatherum elatius*, formerly noted as abundant, has now disappeared; this may be taken, by analogy with other places, to indicate a pronounced local increase in rabbit pressure. There appears to have been a decrease of *Senecio jacobaea* and an increase of *Myosotis arvensis*, but these, not being regular perennials, are liable to fluctuate greatly within a year or two—a phenomenon often conspicuous in *S. jacobaea*.

Attention may here be drawn to the contrast between Phots. 21 and 22. These show the turf on the southern slope of Ramsdean Down to be considerably more broken recently than in 1921. The growth of the bushes in the valley is striking. All of those visible when the later photograph was taken in 1940 were elders (*Sambucus nigra*). Why this development should have occurred during this particular interval of time it is impossible to say with any certainty. There used to be sheep on the hill until about the time of the 1914–18 war, or possibly a little before it (traces of terracing are visible in Phot. 21), and in this connection the opinion of the bailiff who has worked in the neighbourhood for many years is interesting. He holds that the treading down of the turf by the sheep has a very important effect in keeping it intact and preventing rabbit-scraping and subsequent frost from destroying it. The disruption of the turf, which is shown by Phot. 21 to have occurred by 1921, may at that time have been too recent for a full invasion by *Sambucus*, whose successful establishment waits upon the destruction of turf. The central line of the valley, whose turf has probably been more trodden than that on either side, and occupies flatter ground not subject to the same erosion as the slopes, is devoid of bushes.

Although the valley just alluded to, and also the adjoining north slope of Ramsdean Down (HB 16), appear to have undergone an increase in rabbit attack, the southern slopes of Butser Hill are now much less severely grazed than in 1921. At the head of Wascombe Bottom a continuous fescue turf composed mainly of *Festuca rubra* has formed on the north-east-facing slope seen in the foreground of Phots. 23 and 24. On the drier south-facing slopes seen in the background an open cover has appeared, of which the principal constituents are *Leontodon hispidus*, *Ranunculus repens*, *Senecio jacobaea*, *Inula conyza* and *Cirsium palustre*. The group of recolonizing yews noted by Watt (1926) is spreading actively, many of the small bushes in the open having grown up out of the reach of rabbits so that their future seems assured.

A similar recovery from rabbit devastation is indicated by Phots. 25 and

26, taken at the head of Hillhampton Bottom, the next combe to the north-east of Wascombe Bottom.

HB 18. *Butser Hill, south-east slope,* 29 *September* 1936 *and* 26 *July* 1938

The second survey almost certainly covered much of the same ground as the first. Slope 20°. Turf short, but grazing (by rabbits) is not heavy and has probably diminished, as in the two neighbouring areas just mentioned.

Species in common, 1920 and 1936—69 % of shorter list; the same percentage is given by a comparison of the 1920 list with that of 1938.

By comparing the 1920 list with two independent lists made in the second survey (dates above), it is possible to conclude that the following changes have occurred: Decrease of *Avena pubescens, Brachythecium purum, Camptothecium lutescens, Neckera crispa, Cladonia fimbriata*; increase of *Bellis perennis, Hieracium pilosella, Plantago lanceolata, Dicranum scoparium.*

HB 19. *Windmill Hill, north slope*

Lists suitable for comparison are not available for this area. The rabbit-devastated vegetation, containing much *Sedum acre* and *Helianthemum nummularium,* has remained essentially unaltered since 1920.

3. *Cocking,* 9 *August* 1935

Escarpment, north-west slope *c.* 18°, with beechwood and calcicolous coppice on one side. Considerably grazed, mainly by rabbits. Less *Festuca* than usual. The identification is not quite certain, but if, as is very probable, the area examined in the second survey is the original one, there seems to have been some diminution in grazing intensity, although it is still considerable.

Species in common, 1921 and 1935—72 % of shorter list.

Carex flacca, which was 'almost dominant' in 1921, remains very prominent, but *Poterium sanguisorba* has increased and become at least equally important. *Hippocrepis comosa* has decreased.

4. *Heyshott,* 8 *August* 1935

Identification exact. Escarpment, north slope 32°, bounded on either side by chalk scrub developing to young ashwood. Herbage severely rabbit-eaten with mosses very prominent. The description given in Studies IV, pp. 5–6, still applies in nearly every detail, the heavy grazing by rabbits having remained in force.

Species in common, 1921 and 1935—81 % of shorter list.

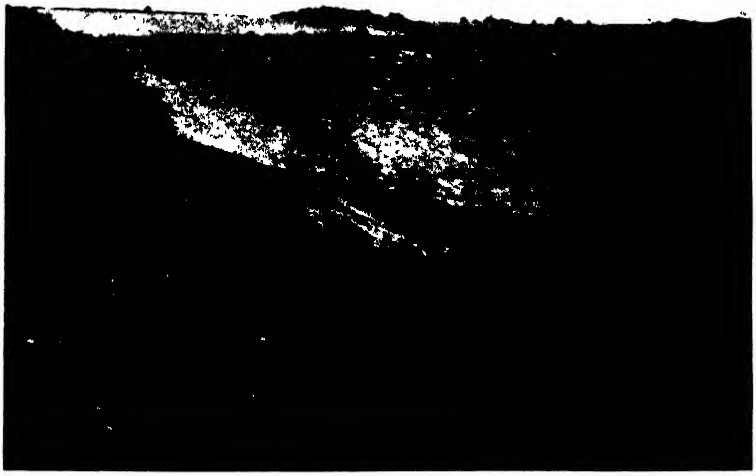
The only clear difference from the 1921 condition is the diminution of the large clumps of *Dicranum scoparium,* but *Poterium sanguisorba* has probably also decreased.

The grassland of this area is evidently in a very stable state. The proportion of species common to the first and second survey lists is high. Also the frequency symbols differ much less than usual, the 'disagreement' class (p. 220) amounting to only 15 % of the total flora, as against the average figure of about 28 % obtained in comparing the two surveys. Three of the less constant bryophytes noted in the first survey, namely *Hypnum cupressiforme* var. *elatum, Neckera crispa* and *Frullania tamarisci,* are still present.

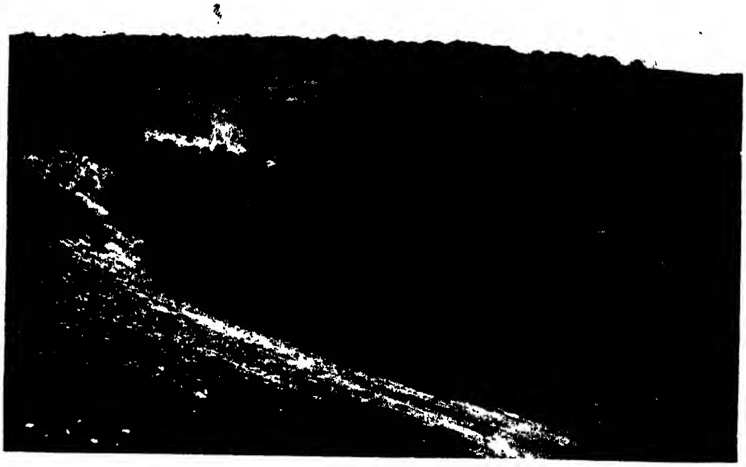
Phot. 21. South-facing slope of Rams-lean Down, Butser Hill, April 1921. Traces of terraces formerly made by sheep are faintly visible on the right. (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. VI, phot. 4.)

Phot. 22. The same, 7 May 1940. Turf somewhat more broken than that shown in Phot. 21. The extensive new growth of bushes in the bottom and on the slope is all *Sambucus nigra*. Higher up the slope, some of the small bushes (juniper) have died, the dead remnants of them which still exist being invisible in this photograph.

Phot. 23. Head of Wascombe Bottom, Butser Hill, April 1921. The bare chalk is the result of rabbit devastation. *Teucrium scorodonia* in foreground. 'On the right appear yews recolonizing the area' (Watt, 1926). (Phot. A. G. Tansley. *J. Ecol.* **13**, Pl. VI, phot. 3.)



Phot. 24. The same, 7 May 1940. Closed fescue turf with ant-heaps on left. Open herbaceous colonization in background, centre. The black dots are young yews.



Phot. 25. Head of Hillhampton Bottom, Butser Hill, April 1921 Turf much destroyed by rabbits in foreground and distance. (Phot. A. G. Tansley *J. Ecol.* **9**, Pl. X, Fig. 2.)

Phot. 26. The same, 19 April 1940. The turf, largely composed of *Festuca ovina*, has recovered considerably. The growth of the yews is noticeable, but apparently no new bushes have established themselves.

5. *East Dean, west-facing slope*, 7 *August* 1935 (*and* 2 *September* 1939)

Identification approximate. Roadside, slope 10°. Sometimes lightly pastured. Herbage well grown, rather mixed. In 1935 it had apparently been grazed more heavily, by cattle and rabbits, than in 1921.

Species in common, 1921 and 1935—87% of shorter list.

Thus the flora has remained very much the same. Nor have there been any noteworthy changes in abundance, although an increase in the fine-leaved fescues appears probable.

When examined in 1939 the herbage was taller again, and *Dactylis glomerata* had increased considerably, to co-dominance in several large patches.

6. *East Dean, east-facing slope*, 1 *September* 1939

Pastured field, slope 10–12°. In 1935 the area was incorrectly identified. On another visit made in 1939 it was located very closely, there being only one rather small expanse of grassland in the field concerned where the angle of slope tallied with the 1921 record. The interval of time is thus 18 years. The turf has been eaten down since 1921 from 10 cm. to about 3 cm. The predominant grazing animals are sheep.

Species in common, 1921 and 1939—80% of shorter list.

Bromus erectus, formerly occasional, has disappeared from the area, although it occurs sparsely on the north-east slope of the same field. There has also been a decrease of *Bellis perennis*.

10–11. *Amberley Mount, west-north-west slope*, 1 *August* 1935

It was impossible to recognize the areas 10 and 11 individually, since they were very close together. On the second survey a single area was listed, probably between the sites of the original 10 and 11. For comparison the separate 1921 lists of 10 and 11, which differ but little, have been combined and average frequency values derived.

Escarpment, slope 20–25°. The herbage, thick and ungrazed in 1921, is now thinner and moderately grazed by sheep and rabbits, and patchy in appearance, usually a sign that there has been a recent onset of grazing. There is no longer a notable number of tall grass inflorescences as in 1920. Scattered *Crataegus* as before.

Species common to the 1921 list for area 11 (longer than that of area 10) and the 1935 list for 10–11—85% of shorter list.

There have been no distinct changes in the abundance of any species.

12. *Amberley Mount, north slope*, 1 *August* 1935

Identified quite closely. Escarpment, slope 18–25°. Turf now tussocky, largely composed of *Festuca*; moderately grazed by rabbits. No evidence of any change in factors since 1921.

Species in common, 1921 and 1935—79% of shorter list.

Centaurea nemoralis, *Leontodon hispidus* and *Succisa pratensis* have decreased, *Dicranum scoparium* increased.

13. *Amberley Mount, north slope*, 1 *August* 1935

Approximately identified. Escarpment, slope 22–32°. Turf considerably rabbit-eaten. No evidence of change in factors since 1921.

Species in common, 1921 and 1935—80% of shorter list.

Considerable increase in *Poterium sanguisorba*.

14. *Rackham Hill, north slope*, 31 *July* 1935

Closely identified. Escarpment, slope 32–37°, with isolated bushes of juniper, etc. Scarcely grazed in 1921. There has been a pronounced onset of rabbit-grazing since then, but compared with many areas the turf is still only lightly grazed. The herbage, which was previously 25–45 cm. tall with inflorescences of 30–60 cm., is now composed of large tussocks 18–28 cm. in height with turf between them only 5 cm. thick. There are now few grass stalks which have not been bitten off short. General appearance homogeneous.

Species in common, 1921 and 1935—74% of shorter list.

Poterium sanguisorba has increased. Apart from this change, the effects of bringing this previously ungrazed grassland to a level of light grazing seem to have been small, so far as the abundance of the principal species is concerned.

16. *Chanctonbury, north slope*, 24 *July* 1935

Exactly identified. Escarpment, slope 27°. Conditions apparently unchanged; considerably grazed by rabbits.

Species in common, 1921 and 1935—89% of shorter list.

There has probably been a decrease of *Bellis perennis* and *Carex flacca* and an increase of *Dactylis glomerata*, but the second survey records for this area are less reliable than the average.

17. *Steyning Round Hill, north slope*, 25 *July* 1935

Area identified fairly closely. Escarpment, slope 27°. Scattered junipers. Much *Bromus erectus* in the herbage, patches of *Brachypodium pinnatum*. In the latter the herbage is about the same depth (23–30 cm.) as in 1921, when it was noted as 'deep and thick'. Elsewhere the turf is now only 5–7·5 cm. deep, and is quite heavily grazed by rabbits and cattle—evidently a considerable increase of grazing. The turf has been a good deal broken, exposing soil and chalk lumps.

Species in common, 1921 and 1935—82% of shorter list.

There is one well-attested change; *Bromus erectus*, although abundant, is no longer dominant on the *Brachypodium*-free areas. The field notes of 1935 state that these areas have no single dominant species.

18. *Steyning, south-east slope*, 25 *July* 1935

This area, on a slope of 5° bearing scattered shrubs, could not be located exactly, but three places were examined of which one almost certainly was the original. Whichever was the exact site, the same change seems to have occurred since 1921, viz. a wide increase of *Brachypodium pinnatum* (local in 1921), leaving spaces between occupied by a grazed turf.

19. *Tottington Hill, north slope*, 26 *July* 1935 *and* 12 *June* 1936

Escarpment, slope 15–25°. Scattered *Crataegus* bushes. Pastured at the time of the second survey. The site was on a broad hillside and the two surveys may not have covered the same ground. The vegetation is, however, uniform over a large area. Over a smaller area it is by no means uniform, apparently as a result of considerable recent grazing by horses as well as cattle and rabbits. The turf in some places is much eaten down while in others it is relatively untouched. The dung of the cattle and horses has produced patches of dark green herbage

— a typical feature when their grazing has started only recently. The turf generally is about 6 cm. thick, with tufts of *Bromus erectus* about 20 cm. high. 15–20 cm. is mentioned in Studies IV to be the general height of the herbage on this area of 'very good uniform grassland'. It therefore seems certain that it is now grazed more heavily than it was and, to judge from the present patchy effect, that the onset is recent.

. Species in common, 1921 and 1935–6—85% of shorter list. (The second survey list used was obtained by combining the results of two separate visits, dates above.)

By comparing the first survey list with those of 1935 and of 1936 separately, and from the notes made in the two surveys, it may be concluded that there has been a definite decrease of *Avena pratensis* and increase of *Festuca ovina+rubra*. It is also very probable that *Achillea millefolium* has decreased and *Succisa pratensis* increased.

20. *Truleigh Hill, north slope*, 12 *June* 1936

Identification probably fairly accurate. Escarpment, slope 30–32°. The conditions appear to be about the same as in 1921; at present ungrazed.

Species in common, 1921 and 1936—78% of shorter list.

There is no reliable evidence of any changes in abundance.

21. *Edburton Hill, north slope*. 28 *July* 1935

Escarpment, slope 30–35°. Sheep pasture. The exact area could not be distinguished with certainty. Three concave slopes of the angle specified in Studies IV were examined, and it is almost certain that one of these was the site of the first survey. In each case there was much less *Poterium* than in 1921. A decrease of *Poa pratensis* and an increase of *Deschampsia caespitosa* are also probable. There is no evidence available as to any change of local factors; sheep are now grazed regularly on this part of the escarpment.

22. *Perching Hill, north slope*, 29 *July* 1935

Closely identified. Escarpment, slope 32–37°. Sheep, which grazed the area in 1921, still do so, but apparently more lightly; the sheep-trodden terraces are less pronounced than in that year, when the grazed herbage on the terraces was noted as 2·5 cm. thick and the tall grasses between them as 30 cm. Now the extremes are 5 and 13 cm. respectively.

Species in common, 1921 and 1935—83% of shorter list.

The number of species with first and second survey records showing 'disagreement' (p. 220) is only 20% of the total flora, and since, under the conditions of recording which here apply, a 23% disagreement may be reached purely by error (Hope-Simpson, 1940*a*), no specific changes can in the present case be stated to have occurred.

23. *Between Perching and Fulking Hills, north slope*, 29 *July* 1935

Identified exactly. An unusually steep slope of 37–40° on the face of the escarpment, probably caused artificially in making a path which slants down the hill just below the area. At present ungrazed, as was probably the case in 1921. On inspection in 1935 Prof. Tansley considered that the slope, which in 1921 was presumed to be in a late stage of colonization consequent on cutting the path, was more fully covered than previously. The cover is now complete, except where, on the lower part of the area, there are little short ledges whose almost vertical face, overhung by *Neckera crispa*, is bare of vegetation. The upper part of the area bears a growth of tall grasses 18–20 cm. thick. The general appearance, except where *Arrhenatherum* is dominant, is almost that of mature chalk grassland.

Species in common, 1921 and 1935—78% of shorter list.

In general the recorded changes in frequency are slight, but it is well substantiated that *Poterium sanguisorba* and *Tussilago farfara* have both decreased; according to the records the latter has disappeared from the area, an occurrence to be expected sooner or later in a community representing a late stage in colonization of bare chalk.

24. *Fulking Hill, north-east slope,* 29 *July* 1935

Escarpment, slope 22–24°. Ungrazed. This area could not be identified closely. The grassland is so variable on the north-east side of Fulking Hill that the list obtained would have depended largely on the exact location. *Arrhenatherum elatius*, absent from the list in Studies IV, is now widespread and has probably increased.

25. *Devil's Dyke, north-north-west slope,* 30 *July* 1935

Identified very closely. Slope *c.* 30°. Grazing, by sheep, is moderate and probably much the same as in 1921, although there may have been a slight increase.

Species in common, 1921 and 1935—78% of shorter list.

Viola hirta has increased in abundance. There seems to have been a decrease in *Knautia arvensis* and a corresponding increase of *Succisa pratensis*, but some confusion between these two is not impossible, since the rosette leaves are somewhat similar. A special search was made for *Primula veris*, recorded as occasional in the first survey. Considering its conspicuous foliage, the failure to find it again may be taken as reliable evidence that it has disappeared from the area.

26. *Devil's Dyke, south-south-east slope,* 30 *July* 1935

Identified very closely. Slope *c.* 30°, opposite area 25. Grazed by sheep. The herbage is about the same depth as in 1921, averaging 4–10 cm. The conditions are probably unaltered.

Species in common, 1921 and 1935—85% of shorter list.

The changes substantiated are a decrease of *Hippocrepis comosa* and an increase of *Bromus erectus*.

27. *Escarpment south of Goat Farm, Westmeston* (*V-plantation*), *north slope,* 14 *June* 1936

The area is exactly defined, being on a slope of 35–37° 'in and above angle of V-shaped plantation' (Studies IV).

There has been a very profound change in treatment since 1921, when the herbage was not grazed and consisted of an exceptionally tall and rank growth of grasses, 20 cm. deep at the top of the area and 45 cm. below. This condition held until 1926 or 1927, when cattle were introduced. They have grazed regularly from that date. In 1936 there was a broken turf 2·5–5 cm. thick with tussocks 10 cm. high. In addition to the cattle, rabbits have been grazing heavily and scratching the ground. The notes of 1936 state that the grasses still easily preponderate in the herbage, especially on the lower part of the area.

Phot. 27. Mount Harry, north slope (area 29), August 1921. Established hawthorn scrub occupies the sheltered sites, and young hawthorns are appearing on the nearer slope (right centre). (Phot. A. G. Tansley. *J. Ecol.* **14**, Pl. I, phot. 1.)

Phot. 28. The same 16 June 1936. The extension of hawthorn scrub in 15 years is clearly seen. That near the camera has grown up so as to hide part of the foreground seen in Phot. 27.

Here the appearance of the herbage is not at all reminiscent of chalk pasture. but rather of neutral grassland.

Species in common, 1921 and 1936—83 % of shorter list.

The changes have been mainly what would be expected to follow the onset of grazing, the short instead of the tall species now dominating. There have been decreases in *Arrhenatherum elatius*, *Avena pratensis*, *A. pubescens*, *Festuca elatior*, *Galium verum* and *Pimpinella saxifraga*. The only distinct increase is in *Festuca rubra* but *Agrostis* has probably also increased.

Several species are still present which are clearly relics from the previous exceptional condition. *Festuca elatior*, although significantly decreased, remains plentiful, and *Centaurea nemoralis* is unusually frequent. *Anthriscus sylvestris*, rare in 1921, is still present in spite of being eaten down. Mosses are less conspicuous than on most grazed and sheltered north slopes, probably because they have not had time to spread since the reduction of the tall grasses which previously suppressed them.

1–4-year seedlings of *Fraxinus excelsior* and *Acer pseudoplatanus*, about 5 cm. high, occur in the grazed turf.

29. *Mount Harry, north slope*, 16 *June* 1936

The general location of the area, occupying a slope of 30° on the escarpment. is not in doubt, but the boundaries of the ground surveyed may have differed a good deal on the two occasions.

The herbage, which was noted in 1921 as cattle-pastured and 15–20 cm. thick, now appears to be scarcely grazed except locally by rabbits, and tussocks up to 28 cm. are common. A recession of grazing is also suggested by a comparison of Phots. 27 and 28, which show that between 1921 and 1936 the grazing has been slight enough to allow a very pronounced spread of hawthorn scrub. A careful examination of individual shrubs in the two photographs suggests that in 1921 the pronounced growth of scrub on the convex middle slope had just started, presumably spreading from the scrub centres in the sheltered concave slope and the lip of the escarpment. This would date the cessation of pronounced grazing at about 1916, when in fact sheep flocks were greatly diminished on many parts of the downs owing to the war of 1914–18. The first survey was therefore made on a pasture regularly grazed until about 5 years before and still grazed to some extent, and the second survey on the same pasture after about 20 years of under-grazing.

Species in common, 1921 and 1936—85 % of shorter list.

In spite of the changed conditions, the lists are floristically similar, and there have been no really striking changes in frequency. Lesser changes cannot be safely inferred owing to the inexact definition of the area.

30. *Mount Caburn, south slope*, 18 *June* 1936

Identified exactly. South escarpment of isolated group of downs east of Lewes, slope 23–28°. Grazed by sheep from about August to the end of November. Herbage 10–15 cm., rather sparse, *Bromus erectus* preponderating. The general appearance of the area has not changed since 1921. According to a shepherd the flocks of sheep grazing the Mount Caburn group of downs were double their present size in 1914, the reduction occurring during the subsequent war, so that any vegetational change which may have occurred since then may not have proceeded far by 1921. The shepherd also held that although *B. erectus* had 'always' covered this group of downs, it had increased its hold since 1914.

Species in common, 1921 and 1936—68% of shorter list.

Clearly indicated are decreases in *Avena pratensis* and *Scabiosa columbaria* and increases in *Carex flacca*, *Filipendula hexapetala* and *Leontodon hispidus*. It is impossible to say whether these changes have anything to do with the diminution of sheep grazing.

31. *Mount Caburn, north slope*, 18 *June* 1936

Closely identified. Slope 23–25°. Tall Brometum as in 1921. The remarks made under 30 about sheep also apply here; freedom from grazing in spring and early summer accounts for the tall growth of grass observed.

Species in common, 1921 and 1936—69% of shorter list.

Decrease in *Avena pratensis* and *Phyteuma tenerum* (formerly given as *P. orbiculare*).

32. *Cliffe Hill, south slope*, 20 *June* 1936

Closely identified. Slope 18° steepening to 32° downwards. The general appearance is just as described in Studies IV; pronounced terraces made by sheep, *Bromus erectus* herbage 10–23 cm. The same facts about recent sheep grazing apply to this area as to 30.

Species in common, 1921 and 1936—80% of shorter list.

Avena pratensis, *A. pubescens* and *Plantago media* have decreased. The reduction of the last named might reasonably be correlated with the diminished trampling on the terraces by sheep, since it is especially common in trodden turf. *Succisa pratensis* has increased.

33. *Malling Hill, flat top*, 20 *June* 1936

Closely identified. Conditions probably unaltered since 1921 (short pasture).

Species in common, 1921 and 1936—79% of shorter list.

No undoubted changes of frequency.

36. *Firle Beacon, north slope*, 15 *August* 1936

Fairly closely identified. Escarpment, slope 30–32°. Although there has been a general diminution of sheep-grazing in the Firle Beacon locality, the appearance of the herbage compared with the notes in Studies IV suggests that it was less severely eaten down in 1921 than in 1936. The general features of the area—sheep-grazed herbage alternating with big patches of *Brachypodium pinnatum*—are unaltered. A shepherd who was questioned stated, however, that *Brachypodium* has lately been spreading fast, the change being almost visible yearly. He attributed it primarily to the reduction of the sheep flocks, and also admitted that mere burning of the patches, as has been done on this area, does little towards eliminating *Brachypodium*. The same views are held by others acquainted with chalk grazing land.

Species in common, 1921 and 1936—74 % of shorter list.

The records strongly suggest a decrease of *Leontodon hispidus* and increases of *Deschampsia caespitosa*, *Festuca elatior*, *F. ovina* + *rubra* and *Holcus lanatus*, but unfortunately it is impossible to be certain of any of these changes.

37. *Beachy Head, south-east slope*, 17 *August* 1936

The approximate location was certain, being on a slope of 20–24° on the escarpment and immediately overlooking the sea, but the exact expanse of ground covered in the first survey could not be identified with certainty. Two adjacent very similar areas on the south-east slope of Beachy Head were listed in 1936 (37*a* and 37*b*) and the combined data compared with those of 1921.

The turf is now only 1–2 cm. deep with tufts 2·5 cm. high (cf. herbage 1–15 cm. in 1921), and is considerably eaten and scratched by rabbits. The sheep-trodden terraces observed in 1921 are still detectable although not at all a conspicuous feature. These facts suggest that rabbits have increased and that the effects of earlier sheep grazing have been diminishing.

Species in common, 1921 and 1936—72 % of shorter list.

A large number of species—35 % of the total flora—show 'disagreement' (*wide* divergence) between their 1921 and 1936 frequency symbols. Although this is partly due to the inaccurate identification of the area, it seems clear that the following changes must have occurred: Decrease of *Achillea millefolium* and *Trifolium pratense*, and of *Galium verum*, which was specially mentioned as abundant in the first survey, but was sought without being found in the second; increase of *Bellis perennis*, *Filipendula hexapetala*, *Thymus serpyllum*, and probably of bryophytes generally.

40. *Cliff end, flat top*, 16 *August* 1936

Second survey area almost certainly close to the original one. Top of sea cliff, some distance from edge. Herbage 1 cm. The conditions apparently have not altered since 1921.

Species in common, 1921 and 1936—87 % of shorter list.

Cladonia rangiformis was very abundant in 1936. It appears likely that this species was generally called *C. sylvatica* in the first survey, but since neither species is mentioned in the 1921 list for the area, there can be little doubt that *C. rangiformis* has increased. The factors controlling the occurrence of lichens in chalk grassland are by no means clear. In some areas they are very plentiful and it is of course possible that they show a cyclic increase and decrease similar to that demonstrated by Watt (1938) in Breckland, although the contributory factors (notably wind erosion, which is very pronounced in Breckland) are unlikely to have the same proportional influence.

Chalk Heaths (Areas A, B, D). Surface soil slightly acid although derived immediately from chalk, of which lumps sometimes occur at only 5 cm. from the surface. *Calluna* and other more or less calcifuge species are present in association with the usual chalk grassland flora. Areas HB 14 and HB 15 on the summit of War Down (pp. 237–8) are properly classed among the chalk heaths, but they have been more conveniently described with the other areas on War Down.

A. *Heyshott Down, flat top*, 8 *August* 1935

Isolated bushes of *Crataegus*, etc. Heavily grazed by rabbits. The exact area was not certainly identified, but a list made in the most likely place showed floristic composition quite similar to that of 1921 (species in common 78 % of shorter list) and indicated no marked changes in frequency.

A thorough search was made for a place corresponding with that described in Studies IV (p. 12) 'at the highest level of the summit' with *Calluna* 'v.a. to d.' Nothing like this was found, all approximations to Callunetum being heavily eaten down by rabbits with the *Calluna* much suppressed and never approaching great abundance. It may be inferred that there has been a considerable decrease of *Calluna*.

B. *Burton Down, flat top*

This chalk heath, close to woodland and dotted with shrubs, was not located exactly, but all around the probable region the turf is severely grazed, with suppressed *Calluna* as described in Studies IV. Evidently little altered.

D. *Mount Harry, flat top*, 5 *June* 1936

Quite closely identified; the whole of the expanse which must contain the original area has very much the same character as that actually listed in 1936. Occasional bushes of *Ulex europaeus* and *Crataegus*. Considerably grazed.

The conditions appear to be the same as in 1921, herbage of variable thickness, about 1–13 cm. It may however be recalled that for area 29 on the adjacent escarpment there is clear evidence of a decrease in grazing since about

1916 (see p. 245). This was presumably due to a decrease of sheep, which would also affect the present area since it is only a short distance away. Pasturing of cattle was observed in 1921, in addition to rabbits, but in 1936 the latter were apparently largely responsible for the grazing.

Species in common, 1921 and 1936—78% of shorter list.

The only changes indicated are decreases, of *Bellis perennis*, *Prunella vulgaris* and apparently the three Leguminosae *Medicago lupulina*, *Trifolium pratense* and *T. repens*. For the other common legume, *Lotus corniculatus*, the evidence is not conclusive. The decrease of three leguminous species might reasonably be connected with the withdrawal of regular pasturing by stock.

IV. CONCLUSIONS FROM § III

(Areas HB 8 and HB 9 omitted)

The conclusions from areas HB 8 and HB 9 have already been stated separately (pp. 232–4). The present section deals with the information gained from the remaining forty-five areas.

CHANGES IN GRAZING

Changes in grazing pressure on the South Downs from 1920 to 1936, as deduced from the notes made in the two surveys, cannot be expressed in any more general way than the following:

(1) On Butser Hill, action by rabbits has increased on the north-west side and diminished considerably on the southern side.

(2) War Down and Holt Down have been completely free of grazing since 1932 (forestry plantation).

(3) The sheep-pasture downs in the Lewes district are grazed to about the same degree as in 1921, but more lightly than before the war of 1914–18.

(4) Elsewhere differences in grazing activity are manifest on individual areas but the position as a whole is approximately the same.

Pronounced changes in grazing since 1920 on individual areas, omitting the five on War Down where the complete cessation of grazing is exceptional, are summarized in Table 3 (p. 250).

Note on data from parish returns for stock

Some further evidence as to the changes in grazing activity is available in the annual parish returns for sheep and cattle, kindly provided by the statistical branch of the Ministry of Agriculture and Fisheries.

Two main difficulties arise in using these figures as a source of information about the rough grazing land of the downs. In the first place the data, if they are to be relevant to untreated downland, must be taken from parishes which almost exclusively occupy high-lying chalk land, and the parishes must be considered in groups of several together in order to minimize the effect of purely local fluctuations in the population of stock. In the South

Downs these requirements are only present in two or three districts where the range shows its greatest breadth. Secondly, parishes which for these reasons would give reliable data have, in the eastern South Downs, been under special influences (the spread of the suburbs of Brighton, and the afforestation of the Friston area near Eastbourne) which affect the figures for the population of sheep and cattle, although the grasslands actually surveyed were not under these influences. In the western South Downs only one locality (around Chalton and Marden) provides suitable data.

After allowance has been made for such difficulties, the following is the most precise statement possible. As between the fifteen years prior to the first survey (1905–19) and the fifteen years between the two surveys (1920–34), there were in the latter period, on the South Downs as a whole, distinctly fewer sheep (but still more than half the number) and distinctly more cattle (but less than double the number). Adopting the commonly accepted estimate that chalk grassland can carry six sheep to one head of cattle, the figures suggest that quantitatively the total grazing activity of stock has remained approximately the same or diminished slightly. The change from sheep to cattle is however likely to have influenced the herbage a good deal. The differences in grassland composition due to the action of cattle as against sheep over a long period have recently been observed on a downland area in Wiltshire, where a strict comparison was possible, to be considerable.

Table 3. *Pronounced changes in grazing*, 1920–36

HB 10–HB 15 (War Down) omitted

Area	Grazing	
	1920–1	1935–6
Grazing decreased:		
Wascombe Bottom, Butser Hill	Very heavy (rabbits)	Moderate
22	Heavy (sheep)	Moderate
29	Light (cattle)	Ungrazed
Grazing increased:		
HB 5	Almost ungrazed	Moderate (rabbits)
6	Moderate	Heavy (sheep)
10–11	Ungrazed	Moderate (sheep and rabbits)
14	Ungrazed	Light (rabbits)
17	Very light	Moderate (rabbits and cattle)
19	Rather light	Moderately heavy recently (horses, cattle, rabbits)
27	Ungrazed	Heavy (cattle and rabbits)

CHANGES IN VEGETATION

Floristic changes

In the foregoing notes about individual areas, a figure has been given where data are available, showing the number of species held in common by the lists of the first and second surveys as a percentage of the number in the shorter list of the two. The use of this standard as an index of floristic change was explained previously (p. 228).

The areas with clear evidence available as to change in physiognomy may be divided into those showing a distinct change in the appearance of the vegetation, and those which in general character have altered little. The mean percentage figure of species in common for twelve areas showing a distinct change is 75·5, and for twelve areas showing little change, 72·4. These figures are so nearly the same that, unless they be considered a poor criterion of floristic change, the only conclusion possible is that the larger vegetational changes shown in these grasslands after a 15-year interval are not accompanied by any appreciable floristic change in this period, i.e. that the species present at a given time on a particular area tend to remain there for a good many years under changed conditions, even though their abundance may alter greatly with a large change in the character of the herbage.

Dominance

The greatest changes are of course those where the dominants are different in the two surveys. Changes in dominance have occurred in six (13 %) of the forty-seven mature grasslands examined. They are shown in Table 4, which makes it clear, where evidence about grazing is available, that changes in dominance are associated with pronounced changes in grazing pressure.

Table 4. *Changes in dominance*, 1920–36

Area	Dominant species		Change in grazing
	1920–1	1935–6	
HB 10	Mosses	*Festuca rubra*	Heavy → none
Head of Wascombe Bottom, N.E.-facing slope	Much open ground, no general dominant	Mainly *Festuca rubra*	Considerable decrease
17	*Bromus erectus* (+ *Brachypodium pinnatum*)	Mixed, much *Festuca ovina* + *rubra* (+ *Brachypodium pinnatum*)	Considerable increase
18	Mixed, much *Festuca ovina* + *rubra*	Much *Brachypodium pinnatum*	No direct evidence
27	*Festuca elatior*, *Arrhenatherum*, etc.	*Festuca rubra* and *Agrostis*	None → heavy
Near A	Mainly *Calluna*	*Festuca ovina*	No direct evidence; increased grazing inferred

Individual species

Changes in dominance are hardly likely to be deduced incorrectly or to be missed, but, as mentioned earlier (p. 224), the conclusions which it has been safe to draw about other changes on individual areas are a mere fragment of the truth. Furthermore, it would be taking much too simple a view of the complex influences causing change in abundance in individual species, to attempt to extract many straightforward generalizations about the factors responsible for their increases or decreases, even in connexion with grazing, which is the most markedly changing factor over a period such as 15 years. The same degree of increase or of decrease in grazing pressure has different effects on a given species according to the status of other factors, such as (*a*) the rapidity of the change in grazing pressure, (*b*) whether the change is over the range 'negligible to moderate' or 'moderate to heavy', (*c*) whether the grassland occupies a wet or a dry site, (*d*) other plant species present, (*e*) the species of grazing animal. Concrete examples appear below under *Avena pratensis* and *Festuca*.

Changes which have occurred when there is no recorded difference in conditions on the area are probably most often explained by the conditions having altered just before the first survey, thereby setting in train changes in the vegetation which would be much further developed by the time of the second survey.

In spite of these difficulties, however, a tabulation of the specific changes which have been mentioned area by area in the preceding pages, while not worth reproducing, has enabled some more general conclusions to be drawn about the following species. In all of them except one (*Poterium sanguisorba*), it is clear that the changes have been primarily caused by changes in grazing activity.

Avena pratensis.

Changes of frequency are shown on seven areas. On three of them (HB 3, 19, 27) an increase of grazing is correlated with a decrease of *Avena pratensis*, and on one (HB 12) a decrease of grazing with an increase of *A. pratensis* (cf. similar observation at Downley Bottom, Studies III, p. 202). On three areas, however (30, 31, 32), a decrease of grazing has been accompanied by a decrease of *A. pratensis*. Areas 30, 31 and 32 are all Brometa erecti on the Mount Caburn group of downs near Lewes. In the presence of a species such as *Bromus erectus*, less tolerant of grazing but when ungrazed having a higher 'dominance' in the association (Braun-Blanquet & Pavillard, 1922), *Avena pratensis* suffers through competition.

Brachypodium pinnatum.

This grass has newly appeared on area HB 12 (War Down), where grazing animals have been completely excluded since 1932, and has spread on areas 18 (Steyning) and 36 (Firle Beacon). The testimony of many observers in downland regions is that *Brachypodium pinnatum* has extended very considerably in the last few decades, and such evidence as is to be had leaves little doubt that the less regular pasturing of stock is connected with the increase. From an agricultural point of view the position is serious because *Brachypodium* herbage is practically useless and as far as can be ascertained is almost ineradicable except by ploughing (Hope-Simpson, 1940*c*). Ecologically, the apparent irreversibility of *Brachypodium* invasion puts this grass in a unique position among chalk grassland dominants, with the possible exception of *Carex humilis* (south-west Wiltshire only) which may be found to have a similar relation to the grazing factor.

Bromus erectus.

Bromus appears to have spread on area 26 (absent→o.–l.d.), where there is no evidence of a change in local conditions. It has lost dominance on area 17 and disappeared from area 6, these changes doubtless being due to the heavier grazing. Many observations on the downs show that *Bromus* generally succumbs to regular grazing. It can be displaced from its position as the dominant in a period much shorter than the 15 years of the present study. In a case observed on the North Downs in Surrey, a sward with *Bromus* dominant and the fescues frequent has been converted in five years, primarily by rabbits, to Festucetum with small quantities of suppressed *Bromus*.

Festuca ovina + rubra.

The fine-leaved fescues have become more conspicuous on the northern and western sides of War Down (HB 10 and HB 13), where grazing has been abruptly stopped. In each case it is *Festuca rubra* which plays the leading part. From general observations in the Forestry Commission's enclosures it is clear that a sudden and marked diminution of grazing where the herbage has previously been closely cropped by rabbits leads, except in dry situations, to the dominance of *F. rubra*. It is greatly favoured in such circumstances by (*a*) its resistance to heavy grazing, so that it is always plentiful, (*b*) its creeping habit, which enables it quickly to occupy patches of ground bared by rabbits, (*c*) its capacity for tall growth when not grazed. If the reduction of grazing were gradual the dominance of red fescue would probably be less complete, since there would be time for the much slower-growing *Avena pratensis* to reach a state of equilibrium instead of being suddenly overwhelmed.

On areas 19 (Tottington Hill) and 27 (V-plantation), where grazing has become heavier, there has also been an increase of the fescues. In both cases a significant decrease of *Avena pratensis* is recorded, and in one case (27) also of *A. pubescens* and several other tall grasses. That heavier grazing of a lightly or moderately grazed chalk pasture containing many grass species in fair abundance leads towards Festucetum, was of course to be expected from previous knowledge. Apart from the special conditions mentioned above which favour the increase of *Festuca rubra*, it is, speaking generally, conditions of moderately heavy grazing which produce dominance of the two fescues together.

Galium verum.

This species has decreased on three areas (HB 3, 27, 37), in each case with evidence of increased grazing.

Poterium sanguisorba.

Changes in *Poterium* are indicated on six areas, five of which show an increase. On areas 3 and 13 the increase seems to have been considerable. That *Poterium* fluctuates a good deal is bound to be a matter of ecological importance in the community. The significant changes in *Poterium* are not obviously connected with grazing. Indeed an examination of chalk grasslands without a consideration of the time factor shows that abundance in *Poterium* is not simply related to grazing intensity, nor, so far as present knowledge goes, to any easily detected set of conditions.

V. CHANGE IN IMPORTANT SPECIES IN RELATION TO ONE ANOTHER

The frequency estimations of the two surveys can be turned to further account in spite of their errors, by virtue of the fact that they are available for a large number of areas. It has already been pointed out that the differences between the first and second survey records are to a considerable degree due to errors, but if the records from as many as 40 areas are arranged according to any system unrelated to the factors causing the errors, the large and small errors of recorded frequency, above and below the true value, can be expected to be evenly distributed.

In Figs. 3–5 the differences between the first and second survey symbols for a given species (including differences so far discounted as being possibly due only to errors) are arranged in order of magnitude, the largest apparent decreases on the left and the largest apparent increases on the right, the areas concerned being marked below. The differences shown on the same areas by other species are then plotted on the same chart, enabling one to see whether there is any tendency for large decreases or increases of one species to be related to those of another. The vertical distance representing change in frequency is derived from Fig. 1 (p. 223), which gives an approximate standard of comparison for the frequency estimation of the two surveys.

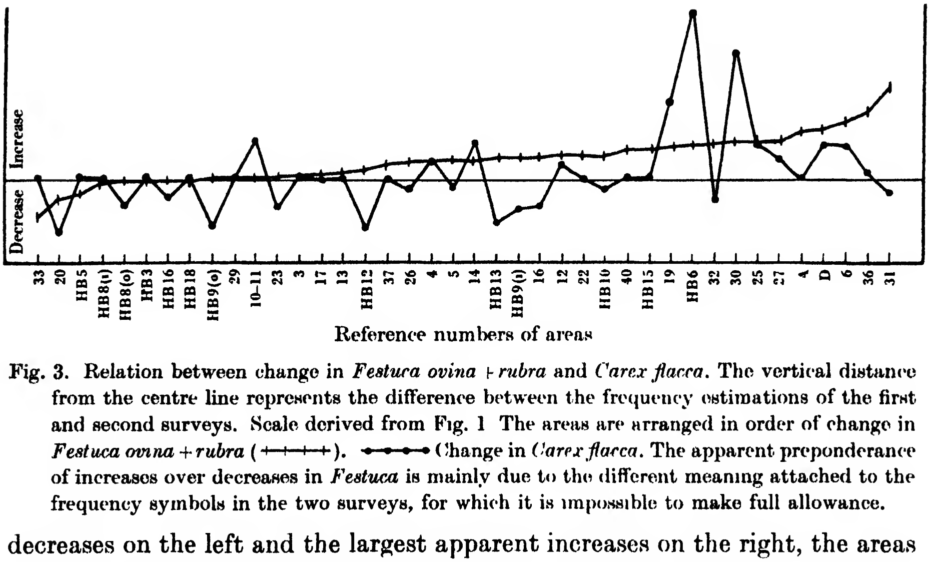


Fig. 3. Relation between change in *Festuca ovina* + *rubra* and *Carex flacca*. The vertical distance from the centre line represents the difference between the frequency estimations of the first and second surveys. Scale derived from Fig. 1 The areas are arranged in order of change in *Festuca ovina* + *rubra* (+—+—+—+). ●—●—●—● Change in *Carex flacca*. The apparent preponderance of increases over decreases in *Festuca* is mainly due to the different meaning attached to the frequency symbols in the two surveys, for which it is impossible to make full allowance.

Fig. 3 gives at least a hint of a relationship between the dynamic behaviour of the fine-leaved fescues and of *Carex flacca*. This of course is only what would be expected from observation of the occurrence of the species, *C. flacca* commonly showing its greatest abundance in Festucetum.

In Fig. 4 changes in *Avena pratensis* form the base line and those of *A. pubescens* plotted alongside run a course which in general is parallel if the great fluctuations due to error are ignored. Again this is not unexpected, but proof from the dynamic aspect has been lacking. A similar relation is shown in Fig. 5 between *A. pratensis* and *Trisetum flavescens*.

The fact that decreases and increases in the abundance of these three grasses are correlated may be taken as partial evidence that they form what has

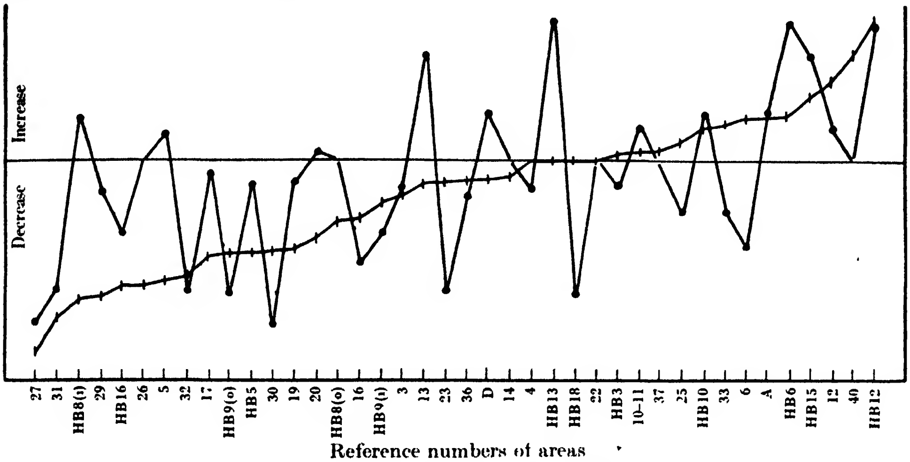


Fig. 4. Relation between change in *Avena pratensis* and *A. pubescens*. Method of plotting as in Fig. 3. The areas are arranged in order of change in *A. pratensis* (+—+—+). ●—●—● Change in *A. pubescens*. Areas against which no point is plotted show no record for the species in either survey.

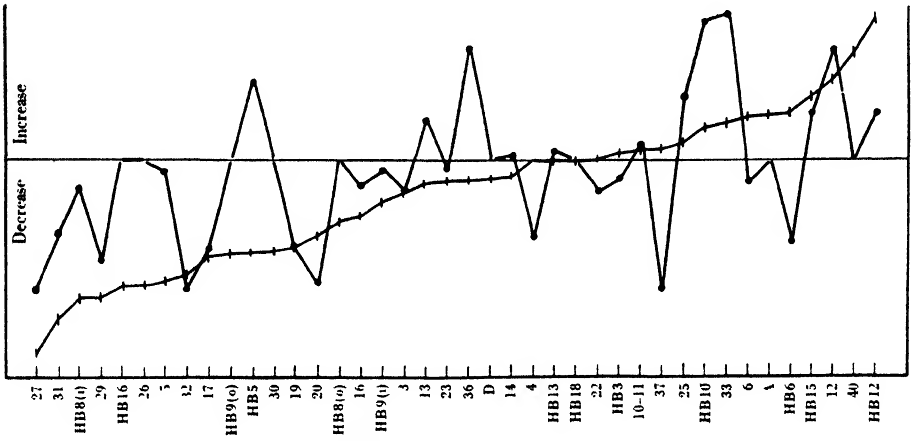


Fig. 5. Relation between change in *Avena pratensis* and *Trisetum flavescens*. Method of plotting as in Fig. 3. The areas are arranged in order of change in *Avena pratensis* (+—+—+). ●—●—● Change in *Trisetum*. Areas against which no point is plotted show no record for the species in either survey.

been termed a synusia (Gams, 1918). Complementary information on the subject would be provided, when frequency data of a more strictly quantitative kind are available, by correlating the abundance of the species of such a group on different areas at any one time.

The same method of plotting changes has also been used for the following species with high average abundance in chalk grassland:

Avena pratensis	against	Festuca ovina + rubra
A. pubescens	,,	,,
A. pratensis + A. pubescens + Trisetum flavescens (added)	,,	,,
Bromus erectus	,,	,,
Poterium sanguisorba	,,	,,
Bromus erectus	,,	Poterium sanguisorba
Plantago lanceolata	,,	,,
Lotus corniculatus	,,	,,
Cirsium acaule	,,	,,
Hieracium pilosella	,,	,,
Lotus corniculatus	,,	Plantago lanceolata
Cirsium acaule	,,	Hieracium pilosella

There is some suggestion of a correlation between increase in *Festuca* and decrease in the synusia of the two Avenae plus *Trisetum*. The only other cases where some relationship is suggested are where *Poterium* was recorded as distinctly more abundant in the second survey, as summarized below (the word 'apparent' should be understood before each mention of decreases or increases, as an admission that errors may in some areas account for the differences between the records):

(1) In the six areas with the greatest increase of *Poterium*, there are five decreases and no increases in *Hieracium pilosella*.

(2) In these six areas and one other with the next greatest increase of *Poterium*, there are three decreases and no increases in *Cirsium acaule*.

(3) In the seven areas referred to under (2), and one other with the next greatest increase of *Poterium*, there is a conspicuous absence of increases in *Plantago lanceolata*.

(4) The facts given above for *Plantago* are also true of *Lotus corniculatus*.

There is thus some hint that an increase of *Poterium* may hinder a simultaneous increase in the four species *Hieracium pilosella*, *Cirsium acaule*, *Plantago lanceolata* and *Lotus corniculatus*. The first three of these species may be noted as plants of rosette or similar habit easily overtopped by *Poterium*, while *Lotus* likewise is not capable of vigorous growth to any great height; in addition *Lotus* and *Cirsium* root in the deeper soil layers, approaching the depth of those exploited by *Poterium* (Anderson, 1927).

VI. SPECIES SHOWING A GENERAL DECREASE OR INCREASE

The following unidirectional changes on several areas are as a whole unrelated to ascertained changes in grazing:

Bellis perennis. In twenty-two areas west of Steyning listed in both surveys, there were thirteen records of *Bellis* in the first survey and only two in the second. East of Steyning the number of records is the same in both surveys. On the areas with a first survey record only, *Bellis* was in every case at least 'occasional'. That the writer cannot detect *Bellis perennis* is hardly an admissible explanation for so many areas, and a substantial decrease in the western South Downs since 1920 may therefore be accepted as a fact.

Leontodon autumnalis. This species, almost confined to the western half of the South Downs, was in the first survey recorded on sixteen and in the second on four of the areas listed in both surveys. Confusion with other Compositae might account for some, but not the major, part of the difference.

Leontodus hispidon. The general frequency of *L. hispidus* has not changed conspicuously, but in five of the eight areas where it was found in the first survey but not in the second, the frequency recorded in the first survey was high (f. or more):

On	1	area(s)	a.	→absent
,,	1	,,	f.–l.a.	,,
,,	3	,,	f.	,,
,,	2	,,	o.	,,
,,	1	,,	l.a.	,,

In the only case of apparently new occurrence (area 40) it has the relatively high symbol f.

From this evidence it seems that *L. hispidus* may be liable to pronounced fluctuation.

Prunella vulgaris. Prunella appeared to be more widely distributed in the eastern half of the South Downs in 1935–6 than in 1920–1. It was recorded on only four of the areas east of Fulking Hill in the first survey, and on ten of them in the second.

Note on rainfall

Weather changes, of which those with most influence on the vegetation are provided by rainfall, are perhaps more likely than any other single factor to account for vegetational changes, such as those in the four species just mentioned, proceeding in the same direction over a wide range of grasslands under varying biotic action. For this reason it may be of interest to give the relevant rainfall data even though no detailed conclusions can be drawn.

As mentioned by Tansley & Adamson (1926), rainfall is higher on the western than on the eastern South Downs. Average figures for the 22-year period 1915–36 are shown below. The annual figures are taken from *British Rainfall* (1915–36). The May–August figures were kindly provided by the Director, Meteorological Office.

	Altitude		Annual rainfall		Summer rainfall (May–August)	
Station	m.	ft.	mm.	in.	mm.	in.
West: Compton, between Petersfield and Chichester	79	259	981·5	38·64	277·6	10·93
East: Jevington, near Eastbourne	84	274	835·9	32·91	231·6	9·12

The effect on the herbage of changes in grazing activity depends to an important degree on the prevailing moisture conditions, as illustrated on War Down (p. 238), and the difference in rainfall between the two ends of the South Downs has doubtless been responsible for some difference in the reaction of the grasslands of these regions to the variations in grazing which have occurred during the period between the two surveys.

It is doubtless summer rather than total annual rainfall which has a decisive influence on chalk grassland vegetation. Fig. 6 shows how the summer rainfall has varied in the periods preceding the two surveys. The difference in its incidence during these two periods is not sufficiently clearly marked to warrant a statement that one survey followed a drier period than the other. Yet it can be seen that its fluctuations over a few years are of a kind which might well alter the abundance of species, like the four mentioned above, showing unidirectional changes on areas under different grazing activity.

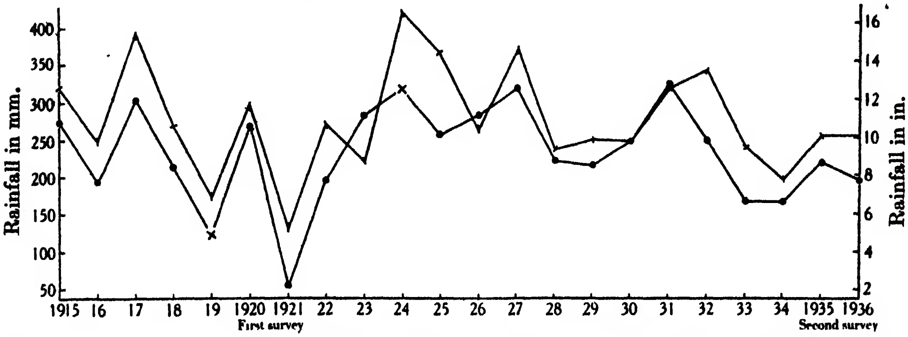


Fig. 6. Summer rainfall (May–August), 1915–36, at stations in the western and eastern South Downs. Figures supplied by courtesy of the Director, Meteorological Office. +——+ W. At Compton, near Petersfield, 79 m. (259 ft.) alt. ●——● E. At Jevington, near Eastbourne, 84 m. (274 ft.) alt. Reliable figures are not available for Jevington in 1919 or 1924; values for the neighbouring stations of West Dean (1919) and Friston (1924) are marked ×.

VII. NEWLY RECORDED SPECIES

Several species recorded from mature chalk grassland during the second survey do not appear in the first survey records of mature grassland. They are listed below in order that, with the lists published in Studies III and IV, there may be a complete record of the chalk grassland flora of the South Downs. Species common in the communities marginal to chalk grassland which are casually found in it but probably not stable are omitted.

- Chalk grasslands:
    - Crepis taraxacifolia
    - Euphorbia exigua
    - Leontodon nudicaulis
    - Orchis mascula
    - Scleropoa rigida
    - Solidago virgaurea
    - Stachys officinalis
    - Valeriana officinalis[1]
  - Bryophytes:
    - Brachythecium rutabulum
    - Bryum caespiticium
    - B. obconicum
    - Ceratodon purpureus
    - Eurhynchium praelongum[1]
    - Hypnum cupressiforme
    - H. cupressiforme var. ericetorum[1]
    - Mnium affine[1]
    - M. stellare
    - Trichostomum crispulum
    - Weisia crispa
    - W. crispata
    - W. tortilis
    - Madotheca laevigata
    - Scapania aspera
  - Lichens:
    - Cladonia pyxidata
    - C. rangiformis
- Chalk heaths (surface soil acid):
    - (Vicia faba)
    - Viola canina
  - Lichen:
    - Peltigera polydactyla

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[1] Recorded by Tansley & Adamson from chalk heath, but not from unleached chalk grassland.

Among these newly recorded species, the only flowering plant of any importance in the association is *Leontodon nudicaulis*, which occasionally, as on areas HB 18 and 37, seems to occupy the place of the usually abundant *L. hispidus*. It is easily mistaken for other of the yellow-flowered Liguliflorae. The new recording of *Crepis taraxacifolia*, although only on two adjacent areas (30 and 31), is likely to be a reflexion of its general spread in the south of England during the last fifty years.

Hypnum cupressiforme, the commonest of the newly recorded mosses, is not at all clearly distinguished from its variety *elatum*, which was frequently recorded in the first survey. Among the acrocarpous moss species, some are occasionally conspicuous, either where the turf is much broken by rabbits, or on very dry southerly slopes, or (*Bryum caespiticium*) where the surface is slightly acid. *Cladonia rangiformis* is the commonest lichen in chalk grassland (Hope-Simpson, 1941). Most of the records of '*Cladonia sylvatica*' in the first survey probably refer to *C. rangiformis*.

VIII. CONCLUSION

Owing to the defects of the methods by which the records of the two surveys have been made and compared, the results extractable from the data are fragmentary. Nevertheless, a study of changes over a number of *large* areas (and therefore by rapid methods of recording frequency) provides information which cannot be obtained in any other way. The repeated examination of permanently marked quadrats of feasible size is often of great value, but the changes seen in them may to a large extent consist of fluctuations occurring in one or a few units of the mosaic of which the vegetation carpet is made, having little to do with any major change in the area as a whole. A single quadrat on a pool in the regeneration complex of a raised bog would show a filling up of the pool during a few years, but would not indicate that the water surface of the bog as a whole was any less. In grassland, a species with a patchy distribution may be present in a permanent quadrat at one time and absent from it at another, without its status on the broad area being materially different. Only by attempting to assess change on the broad area as a whole is there any hope of discovering whether widespread changes occur.

Chalk grassland, although very stable as a whole, is revealed as a community fluctuating on individual areas, but in the period involved in this study the changes amount to an alteration in dominance in only six out of forty-seven mature grasslands (13 %). In chalk grassland, great changes may occur in the herbage without upsetting the position of the commonest dominant, *Festuca* (*ovina*+*rubra*). Nevertheless, the relatively low proportion of changes in dominance in 15 years means that there is no fear of the general picture gained by a survey of semi-natural grasslands on the chalk becoming out of date in a few years' time.

In the cases of change in dominance, and of other major changes (e.g. of the Avenae) there is sufficient evidence to show that alteration in grazing is the principal cause of change. In addition to cases of this type, the two surveys show that abundance has altered in a number of species of greater or lesser importance in the association, but not very much is revealed about the causes of such specific changes; such a revelation could not, of course, be expected from the present study. *Poterium sanguisorba* is the most important species in which changes are shown without clear indications as to the cause.

There is naturally some lag between a change in grazing activity and its full effect on the vegetation, so that at any moment of time the vegetation may not reflect the existing grazing conditions. Similarly, there is a lag, usually much longer, between a change in vegetation and a consequent change in soil. Just as one does not try to relate existing vegetation to the existing grazing conditions without knowing the antecedents, so it is useless in the same ignorance to seek any *close* correlation between vegetation and soil at a given moment. Soil type is of course an exceedingly important factor, and doubtless sets a limit to the alternative vegetation types which different grazing conditions can produce on a particular site.

IX. SUMMARY

This paper presents the results of a second survey, in 1935 and 1936, of forty-seven areas of chalk grassland where records were made by Tansley and Adamson in 1920 and 1921 (Tansley & Adamson, 1925, 1926).

The subjective method of recording which had to be used has necessitated a careful enquiry as to how the data should be interpreted, and the limited conclusions which can be drawn are based on the results of this enquiry.

Two areas at Downley Bottom (A and B) were under periodic observation by Tansley and Adamson from 1908 to 1920. They are considered in some detail because the information is more precise than for the other areas. The enclosures, A and B, erected in 1909 and maintained proof against grazing animals, became derelict about 1924, since when the herbage, like that surrounding, has been grazed largely by rabbits. Outside enclosure A the principal change in the herbage since 1920 has been a spread of casual and wood-edge plants, no doubt partly due to the influence of the scrub established and still flourishing inside the enclosure. *Pastinaca sativa*, which appeared around holes dug in 1919, is now abundant in the turf. Inside enclosure A the scrub which became established in the absence of grazing has had a marked influence on the herbage, in which *Clinopodium vulgare* and *Pastinaca sativa* have increased.

Outside enclosure B the herbage is very much the same as in 1920. Inside the remnants of the enclosure, it is now very similar to that outside, i.e. very different from the condition in 1920. The woody invaders, including *Calluna vulgaris*, have all been killed by the grazing of rabbits. It appears that under

conditions like those at Downley Bottom, heavy grazing can, in a period of about 12 years, largely obliterate the effects of a previous 15-year period of complete freedom from grazing. The abundance of the two thistles, *Cirsium acaule* and *C. palustre*, shown by counts in 1920 to be greater outside enclosure B than inside, still shows a difference as between outside and inside, but in *C. palustre* the 1920 position is now reversed.

On forty-five other areas examined, the influence of grazing was stronger at the time of the first survey in some cases, and of the second in others, while in some there is no evidence of a difference although there may have been changes in the intervening period. Six (13%) of the mature grasslands examined show a change in dominance (Table 4, p. 251). One of these areas is on War Down, where rabbits have been completely eliminated since 1932. On War Down it is shown that a change in the population of grazing animals has a more rapid effect in a moist situation than in a dry one. On the relatively damp north-east-facing slope of Wascombe Bottom a continuous fescue turf has developed where in 1921 much of the surface was bare chalk exposed by rabbits.

Considering species individually, information about change emerges clearly for the three following:

Avena pratensis is discouraged: (*a*) by increased grazing in Festucetum, being replaced by the fescues, (*b*) by decreased grazing in Brometum erecti, since the dominance of *Bromus* becomes more complete.

Festuca rubra (subsp. *genuina*) whose general abundance in chalk grassland has hitherto been overlooked, rapidly assumes dominance on relatively moist areas previously subjected to heavy grazing and suddenly released from it.

Brachypodium pinnatum has spread on the eastern half of the South Downs, very largely because of the diminution of sheep flocks. The agricultural and ecological importance of this occurrence is stressed.

The changes which have taken place in the abundance of certain species are apparently related to those in others. *Carex flacca* has increased most on the areas where the fescues have increased most. *Avena pratensis*, *A. pubescens* and *Trisetum flavescens* on the whole show their largest increases and decreases on the same areas. A pronounced increase of *Poterium sanguisorba* appears (on rather slender evidence) to prevent increases of *Hieracium pilosella*, *Cirsium acaule*, *Plantago lanceolata* and *Lotus corniculatus*. These four species are all of low growth, the first three being plants of rosette or similar habit, while two of them (*Cirsium* and *Lotus*) root in deep soil layers approaching those exploited by *Poterium*.

Four species show noticeable unidirectional changes in abundance (or actual presence), unrelated to grazing, on wide stretches of the South Downs. *Bellis perennis* and *Leontodon autumnalis* are less widespread in the western half than in 1920–1, and *Prunella vulgaris* is more widespread in the eastern half. In more than half the cases where *Leontodon hispidus* appears to have vanished since 1920–1, the frequency recorded in the first survey was high, suggesting that this species may exhibit wide fluctuations in abundance. The difference in occurrence of these four species in the two surveys is presumably related to a widely operating factor such as rainfall.

Chalk grassland, as a whole a very stable community, changes a good deal on individual areas even over short periods (15 years or less) largely through changes in the incidence of grazing.

ACKNOWLEDGEMENTS

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APPENDIX

Table A. HB 8 *and* HB 9. *Downley Bottom, areas A and B*

Records of 1914 (Tansley & Adamson), 1920 (Tansley & Adamson) and 1936. + signifies presence where a frequency estimation was not made. ? signifies probable undetected presence.

	HB 8 (Area A)						HB 9 (Area B)					
	Outside enclosure			Inside enclosure			Outside enclosure			Inside enclosure		
	1914	1920	1936	1914	1920	1936	1914	1920	1936	1914	1920	1936
Aceras anthropophorum	r.	—	—	r.	—	—	—	—	—	—	—	—
Achillea millefolium	a.	f.–l.a.	f.	a.	a. l.d.	a.	f.	f.	a.	f.	v.a.	a.
Agrostis spp.	f.	f.–l.a.	o. l.a.	f.	l.	f.	a.	a.	a. l.c.d.	v.a.	f.	c.d.
Anthoxanthum odoratum	—	—	—	—	—	—	—	o.	—	l.v.a.	l.a.	r.
Asperula cynanchica	f.	f.	r.	a.	o.	r.	a.	o.	o.	f.	—	r.
Avena pratensis	f.	f.	r. l.f.	c.d.	v.a.	r.	f.	f.–l.a.	r.	l.v.a.	f.–a.	o.
A. pubescens	—	—	—	—	—	r.	f.	f.	—	l.	o.	—
Brachypodium sylvaticum	—	—	—	—	—	—	—	—	—	—	r.	—
Briza media	o.	—	v.a.	f.	o.	a.	—	—	a.	f.	o.	—
Bromus erectus	—	—	—	—	—	—	—	—	—	—	l.	—
Calluna vulgaris	—	—	—	—	—	—	—	—	—	l.	l.	(r. dead)
Campanula glomerata	—	r.	—	o.	—	—	—	—	—	—	—	—
C. rotundifolia	f.	a.	f.	f.	f.	f.	o.	o.–f.	a.	o.	o.	a.
Carex flacca	l.s.d.	v.a.–l.d.	a.	c.d.	v.a.	v.a.	v.a.	v.a.	f.	a.	a.	f.
C. caryophyllea	—	o.	r.	?	o.	l.v.a.	o.	l.a.	o.	r.	—	r.
Centaurea nemoralis	—	—	—	—	r.	—	—	—	—	—	—	—
Cerastium vulgatum	—	r.	—	—	—	—	—	o.	—	—	r.	—
Chrysanthemum leucanthemum	—	—	—	—	—	—	—	r.	—	—	—	—
Cirsium acaule	a.	a.	f.	f.	f.	o.	f.	f.	o.–l.f.	o.	o.	r.
C. arvense	—	—	—	—	—	—	—	—	r.	—	—	—
C. lanceolatum	r.	r.	—	r.	—	—	—	—	l.	r.	—	r.
C. palustre	l.a.	f.	f.	a.	l.f.	f.	f.	f.	o.	o.	o.	o.–l.a.
Clinopodium vulgare	l.	l.	o.–l.a.	l.	l.	f. l.a.	—	—	r.	l.	l.	r.
Crepis capillaris	—	—	o.	—	—	l.	—	—	o.	—	—	r.
Cynoglossum officinale	l.	l.r.	r.	—	—	—	—	—	—	—	—	—
Cynosurus cristatus	—	—	—	—	—	—	—	l.	—	—	l.	—
Daucus carota	—	—	—	—	—	—	—	—	—	—	r.	—
Dactylis glomerata	—	—	—	—	r.	—	—	—	—	—	r.	—
Euphrasia brevipila	—	—	—	—	—	—	—	o.	—	—	—	—
E. nemorosa	f.	f.	f.	o.	r.	r.	v.a.	f.	f.	—	—	r.
Festuca ovina + rubra	d.	c.d.	v.a.–d.	c.d.	v.a.–l.d.	v.a.	d.	v.a.	v.a. l.c.d.	d.	a. l.d.	c.d.
Fragaria vesca	l.a.	f. l.a.	o.–f.	l.a.	l.a.	a.	—	—	—	—	—	r.

Table A (*continued*)

	HB 8 (Area A)						HB 9 (Area B)					
	Outside enclosure			Inside enclosure			Outside enclosure			Inside enclosure		
	1914	1920	1936	1914	1920	1936	1914	1920	1936	1914	1920	1936
Galium cruciata	—	—	—	—	—	—	—	—	r.	—	—	—
G. erectum + mollugo	—	r.	r.	r.	l.–l.d.	r.	r.	—	—	r.	l.–l.d.	r.
G. verum	o.–f.	f.	a.	o.	f. l.a.	a.	v.a.	a.	o.	l.d.	v.a.	o.
Gentiana axillaris	o.–r.	o.–r.	o.	o.	r.	—	o.	o.	—	—	—	—
Helianthemum nummularium	—	—	—	—	—	—	a. l.d.	a. l.d.	l.–d.	l.a.	f.	a.
Hieracium pilosella	l.	l.	r.	l.	+	r.	l.a.	l.	r. l.f.	—	—	—
Hippocrepis comosa	—	—	—	—	—	—	?	l.	—	—	—	—
Holcus lanatus	—	—	—	—	—	—	—	—	l.	l.	l.d.	o.
Hypericum hirsutum	—	—	—	—	—	—	—	—	—	—	r.	—
H. perforatum	—	—	—	—	—	—	—	—	—	r.	l.	—
Hypochaeris radicata	—	—	—	—	—	—	—	—	—	r.	—	—
Koeleria cristata	—	—	a.	?	f.	o.	r.	r.	a.	o.	o.	—
Leontodon autumnalis	o.	f.	o.	+	r.	—	o.–f.	o.	—	r.	r.	—
L. hispidus	a.	o.–f.	a.	a.	f.	a.	f.	f.	o.	r.	l.f.	r.
Linum catharticum	f.	o.	—	r.	l.	—	o.	f.	r.	+	r.	—
Lolium perenne	—	—	—	—	—	—	—	—	r.	—	—	—
Lotus corniculatus	a.	v.a.	a.	a.	f.	f.	v.a.	a. l.d.	a.	a.	f.	a.
Luzula campestris	—	—	—	—	—	—	—	o.	o.	—	—	f. l.a.
Medicago lupulina	—	—	—	—	—	—	—	—	r.	—	—	—
Myosotis arvensis	—	—	—	—	r.	—	—	—	r.	—	r.	l.
Origanum vulgare	—	—	—	—	—	—	—	—	—	—	r.	—
Pastinaca sativa	—	—	a.	—	l.a.	v.a.	—	—	—	—	—	—
Phleum pratense	—	—	—	—	—	—	—	—	—	—	r.	—
Pimpinella saxifraga	—	—	—	r.	l.f.	—	—	—	—	—	—	—
Plantago lanceolata	a.	+	f.	a.	o.–f.	a.	f.	f.–a.	o.	f.	f.–l.a.	f.
P. media	—	—	l.	l.	l.	r.	r.	o.	r.	l.	r.	r.
Polygala vulgaris	r.	r.	r.	—	—	r.	r.	?	—	—	—	—
Potentilla erecta	—	o.	—	+	l.	r.	o.–f.	f.	f.	o.	o.–f.	f.
P. sterilis	—	—	r.	—	l.	—	—	—	—	—	—	r.
Poterium sanguisorba	l.a.	l.a.	o.–l.a.	l.a.	a. l.d.	o. l.v.a.	a. l.d.	a. l.d.	f.	f.–v.a.	a. l.d.	f.
Primula veris	—	—	—	r.	r.	r.	+	l.	—	+	r.	—
Prunella vulgaris	o.	o.–f.	f.	f.	o.	o.	o.	o.	f.	o.	o.	a.
Ranunculus bulbosus	—	—	—	—	—	—	r.	r.	—	—	—	—
R. repens	—	—	l.	—	—	r.	—	—	—	—	—	—
Rumex acetosa	—	—	—	—	—	—	—	—	—	r.	r.	—
Scabiosa columbaria	+	o.	o.	f.	f. l.a.	a.	+	o.	—	r.	l.	r.
Senecio erucifolius	—	—	—	r.	l.	l.	—	—	—	—	—	—
S. jacobaea	r.	o.	r.	r.	+	r.	r.	o.	r.	r.	r.	o.

Sieglingia decumbens	—	—	—	—	—	—	—	—	—	—	—	r.
Sonchus asper	—	—	—	—	—	—	—	—	r.	—	r.	—
Succisa pratensis	—	r.	l.	?	+	o. l.a.	—	—	—	—	—	—
Taraxacum spp.	—	—	r.	r.	r.	—	—	—	r.	r.	r.	—
Teucrium scorodonia	—	—	—	—	—	—	—	—	r.	—	—	—
Thymus serpyllum	f.	l.a.	o.	o.	l.	r.	f.	l.a.	f.	o.	l.	r.
Trifolium pratense	f.	o.	r.	r.	r.	—	f.	f.	—	o.	r.	—
T. repens	f.	o.–r.	f.	—	—	—	f.	l.r.	r.	—	—	—
Trisetum flavescens	—	—	—	l.	l.	—	—	—	—	r.	r.	—
Veronica arvensis	—	—	—	—	—	—	—	r.	—	—	r.	—
V. chamaedrys	l.	o.	r.	l.a.	l.	r.	l.a.	l.	r.	o.	r.	r.
V. officinalis	r.	o.	r.	r.	r.	r.	—	—	r.	—	l.	r.
Viola hirta	a.	a.	f.	a.	l.a.	f.–a.	l.a.	l.a.	f. l.a.	f.	f.	f.
V. riviniana + sylvestris	f.	f.–a.	—	o.–f.	o.–f.	r.	f.	r.	r.	o.	l.r.	l.
BRYOPHYTES												
Barbula unguiculata	—	—	—	—	—	—	—	—	a.	—	l.	r.
Brachythecium glareosum	—	—	—	—	—	—	?	—	—	?	o.	—
B. purum	f.	f.	a.	f.	a. l.d.	f.	a.	f.	a.	a.	a.	a.
Bryum caespiticium	—	—	—	—	—	—	—	—	f.	—	—	a.
B. capillare	—	—	—	—	—	—	—	—	—	—	r.	—
Camptothecium lutescens	—	l.	—	—	o.	—	a.	l.	—	o.	o.	—
Dicranum scoparium	a.	l.a.	l.	f.	o.	r.	o.	l.	r.	—	—	—
Eurynchium praelongum	—	—	—	—	—	—	—	—	—	—	o.	—
E. striatum	—	—	—	—	—	—	—	—	r.	—	—	r.
E. swartzii	—	—	—	—	—	—	—	—	—	—	o.–f.	—
Fissidens taxifolius	—	—	—	—	—	—	o.	—	r.	—	—	r.
Hylocomium splendens	a.	f.	r.	a.	f. l.a.	f. l.a.	—	—	—	—	—	—
H. squarrosum	l.s.d.	c.d.	v.a.	l.s.d.	l.s.d.	a.	o.	o.	—	+	f.	r.
H. triquetrum	s.d.	f.–a.	f. l.a.	a.	a. l.d.	a.	a.	a.	l.	+	a.	r.
Hypnum cupressiforme var. elatum	+	l.a.	—	o.	l.	—	r.	—	—	—	—	—
H. cuspidatum	?	o.	f.	f.	o.	o.	—	—	l.	—	o.	—
Mnium affine	—	—	—	—	—	—	—	—	r.	o.	o.	—
Neckera crispa	—	—	—	—	—	—	l.	—	—	—	—	—
Pottia lanceolata	—	—	—	—	—	—	—	—	—	—	r.	—
Thuidium tamariscinum	—	—	—	—	—	—	—	—	—	—	—	r.
LICHENS												
Cladonia fimbriata	—	—	—	—	—	—	o.	—	—	—	—	—
C. sylvatica	—	—	—	—	—	—	l.	—	—	—	—	—
Total number	43	48	48	52	55	46	50	50	53	49	64	46

Table B. *Specific frequencies expressed as percentage, and subjective frequency estimations. Data collected on area* HB 3 (*Chalton Down, east*) *in* 1920 (*Tansley & Adamson*), 1936 *and* 1937

	(Tansley & Adamson) Sept. 1920		25. v. 37	8. ix. 37	25. viii. 36
Aceras anthropophorum	—	r.	—	—	—
Achillea millefolium	8	f.	22	22	o.
Agrimonia eupatoria	0	r.	2	0	r.
Agrostis spp.	4	l.a.	28	38	l.
Anacamptis (Orchis) pyramidalis	—	o.	—	—	—
Anthoxanthum odoratum	4	f.	4	0	r.
Anthyllis vulneraria	2	l.a.	0	0	—
Asperula cynanchica	88	f.	82	80	f.–a.
Avena pratensis	84	l.a.	44	60	f.
A. pubescens	74	l.a.	32	24	o.
Bellis perennis	6	o.	4	2	—
Briza media	42	f.	80	60	—
Bromus erectus	—	l.	—	—	—
Campanula glomerata	—	o.	—	—	—
C. rotundifolia	32	f.–a.	60	74	f.
Carex caryophyllea	22	o.	46	38	f.
C. flacca	92	a.	94	90	a.
Carlina vulgaris	2	o.	6	12	o.
Centaurea nemoralis	—	l.	—	—	—
Cerastium vulgatum	—	l.	—	—	—
Chrysanthemum leucanthemum	8	o.	4	4	r.
Cirsium acaule	98	f.–a.	78	74	a.
C. lanceolatum	—	r.	—	—	—
Clinopodium vulgare	0	l.	6	0	l.
Coeloglossum viride	0	—	2	0	r.
Crepis capillaris	2	l.	0	0	—
Cynoglossum officinale	—	l.	—	—	r.
Cynosurus cristatus	0	—	2	8	—
Dactylis glomerata	—	l.	—	—	r.
Daucus carota	4	o.	2	0	—
Euphrasia nemorosa	2	o.	12	14	o.–l.a.
Festuca ovina	98	v.a.	96	98	v.a.
F. rubra			40	12	
Fragaria vesca	—	l.	—	—	—
Galium cruciata	—	—	—	—	r.
G. erectum + mollugo	0	r.	2	0	r.
G. verum	34	a.	6	10	l.
Gentiana axillaris	0	o.	8	16	o. l.a.
Hieracium pilosella	94	l.a.	76	70	a.
Hippocrepis comosa	0	—	0	4	—
Knautia arvensis	—	o.	—	—	r.
Koeleria cristata	2	f.	86	88	a.
Leontodon autumnalis	22	o.	2	2	—
L. hispidus	100	a.	82	76	a.
Linum catharticum	82	o.	34	36	a.
Lotus corniculatus	98	a.	84	80	a.
Medicago lupulina	4	f.	34	48	o.
Myosotis arvensis	—	l.	—	—	r.
Ononis repens	2	l.f.	36	8	o.–l.a.
Origanum vulgare	—	l.	—	—	—
Phleum pratense	2	l.f.	6	2	—
Pimpinella saxifraga	20	f.	14	8	r.
Plantago lanceolata	78	a.	86	92	a.
P. media	6	o.	16	32	o. l.f.
Poa pratensis	0	—	2	2	—
Polygala vulgaris	4	o.	16	22	r.
Potentilla erecta	—	—	—	—	r.
Poterium sanguisorba	56	o.–l.v.a.	100	90	v.a.
Primula veris	2	l.	2	0	r.
Prunella vulgaris	16	o.	32	32	r.

Table B (*continued*)

	(Tansley & Adamson) Sept. 1920		25. v. 37	8. ix. 37	25. viii. 36
Ranunculus bulbosus	24	o.	64	16	r.
Scabiosa columbaria	78	f.	58	56	f.
Senecio jacobaea	0	r.	4	0	r.
Sieglingia decumbens	0	—	0	2	r.
Spiranthes spiralis	2	o.	0	0	o.
Succisa pratensis	2	o.	0	0	—
Taraxacum spp.	14	o.–f.	12	4	r.
Thymus serpyllum	82	a.	84	74	a.
Trifolium pratense	14	f.–l.a.	54	64	a.
T. repens	0	—	4	4	—
Trisetum flavescens	10	f.	16	2	o.
Veronica chamaedrys	0	—	0	2	—
Vicia cracca	0	—	4	0	—
Viola hirta	0	l.	2	0	l.f.
BRYOPHYTES					
Brachythecium purum	90	a.	68	76	a.
Camptothecium lutescens	34	f.	36	52	r.
Dicranum scoparium	64	f.–a.	0	2	—
Fissidens taxifolius	18	o.	30	18	o.
Hylocomium squarrosum	10	o.	6	4	o.
H. triquetrum	48	l.a.	14	16	f.
Hypnum cupressiforme	0	—	12	26	—
H. cupressiforme var. elatum	14	o.	0	0	—
H. cuspidatum	36	l.f.	32	40	f.
H. molluscum	0	—	10	16	r.
Mnium affine	0	—	2	0	—
Thuidium abietinum	0	—	4	4	r.
Trichostomum crispulum	0	—	8	4	r.
Weisia crispa	0	—	6	4	r.
LICHENS					
Cladonia rangiformis*	0	—	2	10	l.f.
[C. sylvatica]	16	l.f.	0	0	—
Total number	53†	72†	65	58	61†

* This was almost certainly assigned erroneously to *C. sylvatica* in 1920.

† Counting only one for *Festuca ovina* + *rubra*.

THE HYDROSERE AND CURRENT CONCEPTS OF THE CLIMAX

By T. G. TUTIN

(*With two Figures in the text*)

THE THEORETICAL BACKGROUND

Observations made on lakes in Peru by the Percy Sladen Expedition and in the English Lake District have suggested to the author that some revision of the views usually held about the status of aquatic plant communities is necessary in order to fit the facts he has observed in these regions, and possibly the whole field of the synecology of such habitats, more closely.

In order to clarify the approach it is necessary in the first place to decide upon the relative importance of the various factors controlling vegetation and the definition of the climax to be adopted.

It is generally agreed that the chief factors permanently affecting vegetation are climate, geology and topography; history can also be included as the expression of these factors over a period of time. They are interrelated to such an extent that it is nearly impossible to consider them singly, though the attempt has to be made for convenience in measurement and expression.

The effect of climate on vegetation is very evident in the world in general, and the big climatic types of vegetation have been recognized for a long time. Within each type there is a considerable variation not only in floristic composition but also in physiognomy, this variation being due to the influence of one or more of the other factors. These may act in a variety of ways; limestone and millstone grit within the same general climate produce different soils and support different vegetations; one effect of topography is seen in the striking distinctness of the vegetation of a wooded valley and the bare top of the next hill. The effect of geological history is difficult to show with certainty but a comparison of plant communities in England with those in the adjoining parts of Europe at least suggests that many species have failed to reach this country because of the breaking of the land connexion. The existence of types of vegetation no longer capable of regenerating in the place in which they occur is a clearer example of historical influences. Recent history plays a very obvious part in shaping the vegetation of the British Isles, but this is bound up with biotic factors which are usually only of a temporary nature. Nichols (1929) sums up the part played by history in shaping the habitat, and consequently the vegetation, when he says that environmental conditions 'represent the cumulative effect of processes and phenomena which not only have originated in the past, but some of which have long since ceased to operate'.

Similarly, Turner & Watt (1939) suggest that 'the absence of evergreen tree dominants at Killarney may be due to the sifting action of past climates and geographical barriers'.

The foregoing examples will serve to show the efficacy of these factors; the question of their permanence must now be examined.

Climate is known to have changed in many places to a marked extent in a geologically very short period, and there is no reason to believe that change has stopped or that stability is the normal state. The parts of the northern hemisphere which were glaciated during the quaternary ice age still show the effects of it in their topography and even features such as moraines made of soft material remain in a readily recognizable form. During this time the climate has changed from arctic to temperate, passing through intermediate phases of greater warmth, wetness and dryness, so that topography would seem to have at least the same degree of permanence as climate. Geological formations are clearly of great permanence but only affect vegetation indirectly through the part they play in determining soil, topography and climate. Soil type is also determined by climate, topography and vegetation cover and hence will presumably have the same order of permanence as these factors. There would therefore seem to be no reason why climate should be given special prominence among factors controlling vegetation on account of its stability.

The word 'climate' is generally used by ecologists in the meteorologists' sense of a complex of physical factors measured under certain standard conditions. This, as applied to vegetation, is a convenient abstraction but may have little relation to the conditions under which the plants are actually growing unless combined with data about the other environmental factors. The effective climate may be greatly modified by topography and soil. For instance, a south slope may well have a warmer, drier 'climate' than a north slope, and a heavy soil may have an effectively wetter 'climate' than a light soil, even though the actual insolation and rainfall as measured by the meteorologist is the same in the two places. This principle has been recognized in the use of the term microclimate.

It is possible that an unchanging climate acting for a very long period might smooth out differences in topography and soil, but it seems probable that in practice these latter factors change no faster than climate itself.

It might avoid confusion if the word 'climate' were used only in the meteorological sense and the term 'environmental climate' used for the resultant of climatic, topographic and edaphic factors, which is what affects the plant.

At the same time the influence of edaphic factors on the effective climate is not purely physical but depends also on the chemical nature of the soil and especially on the humus content, which itself depends partly on the biological environment. It is clearly impossible to distinguish rigidly between the various aspects of a plant's environment and this grouping of factors, as previously mentioned, should be adopted only for convenience in investigation and expression while aiming finally at as complete an integration as possible.

Climax vegetation is vegetation which is in complete equilibrium with its environment, but since it is probable that this state is rarely if every reached, or if reached it is unlikely that it could be recognized, this definition is largely theoretical. In practice the term is applied to any plant community which appears to be stable and in which there is no reason to believe that important changes are likely to occur in a short time.

There seems to be no reason why the term climax should be restricted to any particular size of community since anything from the largest to the smallest may be in apparent equilibrium with its environment. Clements's concepts of facies and locies within the climax would thus seem to be unnecessary as these are in fact associations or consociations in equilibrium with their environment and therefore climax communities.

The climatic climax (Clements, 1916), which is held by some ecologists to be the only climax, may be described as the type of vegetation which would occur in a given region if climate were the sole determining factor. This type of vegetation is frequently not realized in practice and, as has been shown, there is reason to believe that the causes preventing its realization have the same degree of permanence as the climate tending to produce it. The polyclimax theory is held by those who, implicitly or explicitly, recognize the relative permanence of other factors beside climate and who prefer to use the term climax for any vegetation which is apparently in equilibrium with its actual environment, as opposed to its potential environment, always provided that that environment is not an obviously temporary or unstable one.

Clements's monoclimax theory has the merit of simplicity and has been, and still is, of great value as a stimulus to ecological work, but at the same time it has led many ecologists to attempt to fit every piece of vegetation into a sere leading to the climatic climax and these schemes are frequently completely divorced from reality. Godwin & Conway (1939) have recently shown that the vegetation of raised bogs is in dynamic equilibrium with a complex of climatic, edaphic and topographic factors. Any attempt to fit such a piece of vegetation into a sere relating it to the climatic climax must be entirely artificial and meaningless while, as far as our knowledge goes at present, the polyclimax theory provides a realistic scheme into which it fits naturally.

Until vegetation is much more thoroughly understood on a basis of long experience, it will probably be impossible to decide which if either of these two theories is true, but meanwhile there seems less danger of obscuring facts and a greater probability of inherent truth if the polyclimax view is adopted.

It must be emphasized again that owing to the continuous though slow change in all environmental factors the terms climax and sere are only expressions of the relative rates at which this change occurs, and if a sufficiently long view could be obtained it is almost certain that all vegetation would be seen to be in the process of development. Gleason (1926) has long held such a view. Clements has stated that stabilization is a universal tendency of vegetation, but it is too often forgotten that though the tendency is universal, complete stability is probably rarely if ever attained.

In this connexion it may be pointed out that in the rain forest of the Ivory Coast, Aubréville (1938) has demonstrated the constant change going on in the vegetation. He states (p. 132): 'Les synécies varient non seulement dans l'espace...mais encores dans le temps sans jamais aboutir à un climax définitif.' This flux is due to the inability of the dominants to regenerate in dense shade, and may be paralleled in semi-desert where competition for water prevents regeneration of the perennials except where an old plant has died. Littoral marine animal communities show the same sort of fluctuation (MacGinitie, 1939), and it is probable that such cyclic changes occur in any climax community; the factors causing the change-over from one community to another vary but are probably most often competition for light or water among plants and for food among animals.

In considering the effect of rate of change of environment on plant communities, the rate at which the communities themselves respond to change is of great importance. The length of life of the observer or series of observers will also influence the conclusions drawn. For instance an observer who lived only from one spring to the following winter would be justified in considering the weeds in a fallow field as a climax whose continuance was prevented by an effective alteration in climate. Another observer whose life had lasted since the tertiary might conclude that the present vegetation of north temperate regions was no more stable than the weeds in a field appear to us.

THE AQUATIC ENVIRONMENT

The environmental climate in a submerged habitat differs considerably from that in any terrestrial one, the differences being due to the presence of water and being of a magnitude dependent on the size of the piece of water under consideration. The daily and annual range of temperature and the intensity of the illumination are examples of factors which are profoundly modified in such a habitat. In addition a new factor, that of wave action, is introduced, and this, as has been shown already (Tutin, 1940), plays a large part in controlling the type of bottom and intensity of illumination in the littoral region. In addition there are of course large differences in the chemical environment. The range of variation and degree of stability of these special environmental conditions and consequently of the vegetation living in submerged habitats need to be considered next in an attempt to arrive at conclusions about the status of the various communities present.

In considering the habitat occupied by benthic vegetation wave action is the most characteristic, and in many cases the predominant factor, and consequently may be used as a basis for the classification of the various submerged habitats. Waves occur in all but the smallest bodies of water and their size and the frequency of their occurrence depend in general on the size of the body of water and the strength of the wind, but are also affected by topography. At present it seems only possible to make a qualitative classification into habitats in which waves are of sufficient size and frequency to prevent the growth of rooted vegetation near the shore, and habitats in which they are not. This has been used before (Welch, 1935) as a distinction between lakes and ponds and will be adopted here as the distinction seems to be particularly useful from the biological point of view. All the definitions of lakes and ponds mentioned by Welch suffer from lack of precision, a defect which is inevitable since every intermediate between a pond and a lake occurs in nature. It is possible that when sufficient measurements of wave action and its effect on vegetation have been made, a more precise quantitative definition may be based on them.

It will be convenient in the first place to consider the hypothetical case of a lake and a pond, both with a regular outline, so that complications due to topography may be neglected. The lake basin may have arisen in a variety of ways of which glacial action is the commonest. These are summarized by Russell (1895). In most if not all newly formed lakes the bed is mainly of rock or boulder clay and is free from silt. As such a lake ages it begins to be filled by streams and shore erosion, the rate of silting depending partly on the type of rock in the lake basin (Pearsall, 1921). The importance of silting in the evolution of the lake and the development of the vegetation has been sufficiently stressed by Clements (1916), Pearsall (1921) and Misra (1938) among others; examples of several stages in the process can be seen in the English Lake District. In the absence of large rivers bringing down an abundance of sediment, including particles of large size, and forming a delta, the silt will be swept away from the shores by wave action and surface drift and only deposited where the depth of water is such that water movements are too slow to disturb it. The slope of the bottom will also have an effect on the movement of silt and these two causes will ultimately give rise to a more or less even distribution of sediment over what were originally the deeper parts of the lake. The larger detritus found in the marginal zone of most lakes is slowly broken down and transported by waves to deeper water (Russell, 1895, p. 41). As the level of the bottom near the margin is raised it will come within reach of surface water movements and further deposition will be prevented, fresh sediments being carried farther out. Thus a lake of this sort would not become smaller through the building up of land, but shallower and larger and the depth would tend to become uniform. These changes take place slowly even in humid climates, though they occur more rapidly there than in arid ones (Russell, 1895, p. 90). The glacial lakes in northern Europe and America exist under conditions which tend to produce the most rapid change, but even they have survived many vicissitudes of climate since they were formed at the melting of the ice. During this period the climax land vegetation in the same region has undergone several changes in response to the climate and may well have shown less stability than the submerged vegetation.

In ponds wave action is so slight that silt will be deposited in much shallower water than in lakes and this will provide a substratum suitable for the growth of emergent plants in water sufficiently shallow for their survival. The growth of this reedswamp will protect the shore from erosion, and the detritus of the plants, together with silting, will lead to a relatively rapid disappearance of the pond.

Hence it will be seen that lakes and ponds differ widely in their permanence and that lakes would seem to approach or possibly exceed terrestrial habitats in the duration of a given environmental climate.

The ways in which lakes finally disappear have been discussed by Russell (1895, ch. v), and may for convenience be summarized here and the effect on the vegetation considered. In humid regions sedimentation decreases the depth, but may lead to an increase in area, as in Lake Michigan (Russell, 1895, p. 61), while cutting down of the level of the outflow channel, which is usually slow compared with the former process, leads to a decrease in volume and area. Most probably the last stage in the life of such a lake is a shallow body of water in which wave action disturbs the bottom and interferes with, or prevents, the growth of rooted plants over most of the area. As sediment accumulates or the level of the outflow is cut down still further the water becomes too shallow for large waves to be produced, reedswamp develops and the lake ceases to exist.

In arid regions silting is much slower and there is usually no outflow to the lake. In these regions lakes are subject to large changes in area with seasonal changes in rainfall and usually show traces of still larger alterations in size with fluctuations in climate. Most of these lakes are very flat bottomed and have evidently existed for a long period. As they approach extinction they usually become so salt that vegetation is destroyed and a salt desert remains which is colonized afresh by halophytes.

It will therefore be seen that lakes present a habitat of considerable stability clearly marked off from the surrounding land by the environmental climate and chemical environment. Real lakes differ from the hypothetical bodies of water which have so far been considered in having irregular shore lines so that in certain parts of the littoral region wave action is modified by topography to such an extent that pond-like conditions occur. In these sheltered bays reedswamp is established and filling up proceeds rapidly, as in ponds. That this is a local phenomenon, resulting only in the smoothing out of irregularities, has been shown by Lewis (1938), who points out that a shore is stable when it lies at right angles to the direction of motion of the prevalent waves. The smoothing out of irregularities in the shore line is sometimes accelerated by the formation of sand or shingle spits; excellent examples of this occur on the south shore of Lake Ontario and at the west end of Lake Superior.

In view of the stability and distinctness of the lake habitat it is reasonable to regard some of the aquatic plant communities as being climaxes. The most stable type of submerged environment seems to be one which has silted up until the water is of such a depth that wave action is just beginning to be felt. It is unlikely that a progressive change will occur within a limited time though there may be cyclic changes owing to the plants protecting the silt from erosion, with the result that it will accumulate till the plants themselves are removed by wave action owing to the shallowing of the water. Erosion will presumably then occur followed by recolonization by the original type of vegetation. Thus the equilibrium may be of a dynamic kind as it is in a raised bog.

The usual nature of the sere and the climax in lakes will be illustrated by reference to the ecology of the rooted plants in Lake Titicaca and to a lesser extent in some other lakes. A primitive lake with a rocky bottom will be devoid of macrophytic vegetation, but as silting proceeds the larger plants will be able to colonize certain areas. It is probable that cryptogams, particularly algae, play a pioneer role on rocky shores, just as lichens do in the xerosere, but too little is known about this for any definite statement to be made at present. The first colonists of a new lake are presumably to be looked for among the species found in the least silted habitats or in the lowest light intensities in a more highly evolved lake. In Titicaca the lightly silted regions in good illumination are colonized by the *Zannichellia-Potamogeton* community, and the areas where the illumination is too low for this are occupied by the moss *Sciaromium* or by species of *Chara*. In the English Lakes, as Pearsall has pointed out (1917, 1918), the pioneer communities consist of *Isoetes* or *Littorella* and *Lobelia Dortmanna*, and a Characetum has been described from the deeper water of Lake St Clair (Pieters, 1894). Juday (1934) records the occurrence of *Oscillatoria prolifica*, growing apparently as a saprophyte, at depths of 65–68 m. in a lake in Wisconsin, and further investigation may show that such algae are generally pioneers in the lowest light intensities. These communities will increase the rate of silting by checking water movements and will also add organic matter to the substratum. With the increase in the amount of silt other, generally larger, species come in where the light intensity is high enough. In the lower regions the bottom will be slowly built up by silt and organic detritus till owing to the shallowing of the water the illumination has increased sufficiently to allow this region to be invaded by other species. Consequently there is a succession from the two extremes of low light intensity and poor substratum to a mean with good illumination and a rich substratum, and as in other successions the less exacting species of plants will be replaced by the more exacting. The climax in Lake Titicaca is the *Myriophyllum-Elodea* community which grows to a greater size and contains a greater number of species than any other community in the lake. The relations between the various communities in the lake are summarized in Fig. 1 and in a generalized form in Fig. 2. Similar communities are found in other lakes, sometimes with the dominant species varying from place to place with differences in the bottom deposits just as the dominant species in woodland vary according to the soils.

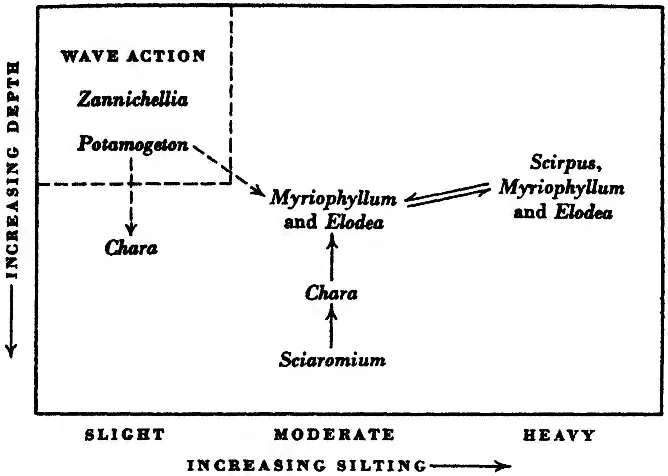

Fig. 1. The relations of the communities in Lake Titicaca.

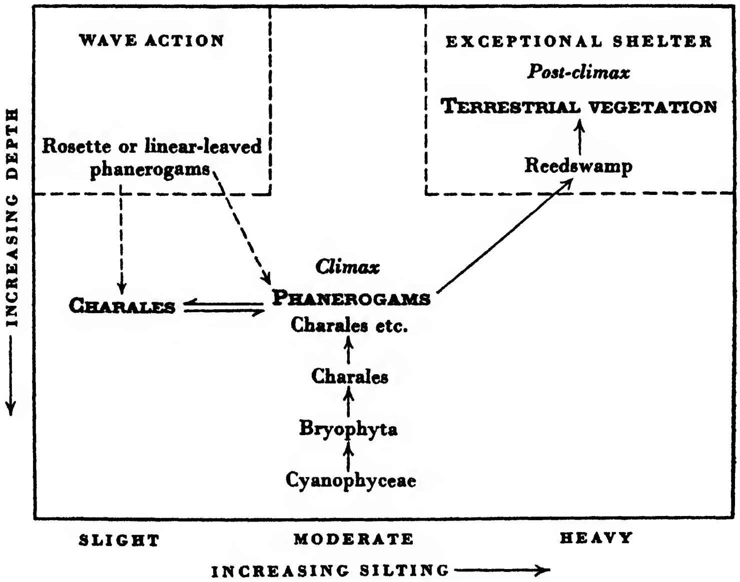

Fig. 2. Generalized scheme of the relations of aquatic plant communities.

In regions where grassland is the general climax the vicinity of water-courses and other specially favourable localities allows the development of post-climax forest in small areas, and similarly sheltered bays in lakes may ultimately lead to the post-climax development of land vegetation. As was pointed out above, Lewis (1938) has shown that any shore tends to lie at right angles to the direction of motion of the prevalent waves as it is stable when it has arrived at this state. This means that a bay in a lake liable to wave action can fill up but, as long as conditions do not alter, a projection will not form and so the extent of the development of the post-climax is strictly limited by the original extent of the exceptionally favourable conditions.

A sere ending in a climax under water is clearly distinct from a hydrosere as usually understood and may conveniently be distinguished by the name limnosere. The term hydrosere may then be kept strictly for a succession starting in a small body of water, or in water-logged soil, and leading to terrestrial vegetation.

It is of interest in this connexion to examine a few of the instances of hydroseres which have been described as starting in lakes. Pearsall (1921) has described the plant successions in the English Lakes and has produced evidence to show how these may be related to the general evolution of the lake basins concerned. At present the successions from attached and submerged plants to terrestrial vegetation appear to be confined to the sheltered shores in the larger lakes, for the greater part of the shore line is wave beaten and the vegetation in a comparatively stable state, the development of emergent communities being inhibited. Several examples of hydroseres in North American lakes are mentioned by Clements (1916, p. 195) and of these the two successions described by Jennings (1908, 1909) may be taken as typical. These two successions occur on the coasts of Lake Erie and the following stages are recognized: lagoon → marsh → thicket → forest in one, and bay → marsh → thicket → forest in the other, but it will be noticed that no succession is described from the coast of the lake as defined above, or indeed from the greater part of the lake no matter what definition be adopted. The same is true of Sweeney Lake, Wisconsin, as described by Wilson (1937), and this author further remarks of Little John Lake in the same region that 'the fluctuation in water level increases the area of wave work upon the shores and only the coarser inorganic soils remain fixed', thus implicitly recognizing that under present conditions there is no seral connexion between the water vegetation and that of the land on such shores, since a bare zone must always intervene.

Such a bare zone, testifying to the effectiveness of wave action may be clearly seen, particularly at a time when the water level is low, in the English lakes. On all but the most sheltered shores there is a zone of stones, rock or clay bounded on the landward side by a small cliff a few inches high, on top of which a wet soil community of *Juncus*, *Carex* and various grasses occurs. This community occasionally invades the edge of the bare zone, but the invasion is from above downwards, is limited in extent and duration and does not appear to have any successional relation to the submerged *Isoetes-Littorella* sward.

The additional effect of variations in water level in making the discontinuity of land and water vegetation more marked is well described by Thoreau (1854), who records long period observations on this variation in Walden Pond, Massachusetts, together with other observations of interest to the hydrobiologist.

Lake Poopó on the Andean plateau in Bolivia and the Balaton in Hungary are good examples of lakes which may be described as senile. Lake Poopó is decreasing owing to evaporation and the salinity of the water has become too great for the usual fresh-water species to persist, but their place has been taken by other plants of the same general character. A large part of the lake is very shallow (2–3 m.) and, with a moderate wind, waves are produced which stir up the bottom at this depth, so that on most days there is a more or less imperceptible gradation from the water to the substratum, which is therefore too unstable to allow the growth of rooted plants. In the Balaton the water is fresh and the accumulation of sand, mainly wind-borne, is filling up the lake. The depth range is much the same as in Poopó and strong gales are frequent, even in summer, the wind always blowing from the north or northwest (Moon, 1934). On the northern side there is a certain amount of submerged vegetation which, in calm periods, invades the edge of the exposed part of the lake but is torn up and cast ashore in great quantities during gales (Moon, 1934; Entz, 1936). If the gales did not always come from the same direction it seems unlikely that any vegetation could exist under water in this lake in its present condition. In Poopó no rooted vegetation was seen growing within 2 km. of the shore though it was cast up in abundance, and it seems safe to draw the conclusion that it maintains a somewhat precarious foothold in the deeper parts of the lake.

When wave action ceases to be effective owing to the small size of the body of water left, the remains of the climax vegetation of the lake may form the starting point of a hydrosere. This, however, does not prevent such a submerged community being regarded as a climax in the lake for, as Tansley (1939, p. 234) says: 'It must be recognized that a given community may change its status from seral to climax or vice versa when there is an effective change in its environmental conditions.'

The type of environmental climate found in lakes occurs in the sea in a more extreme form and the discontinuity of the vegetation of the water and land is very pronounced; in spite of this ecologists have tended to regard the succession of *Zostera*, *Salicornia*, *Glyceria*, etc. culminating in a terrestrial climax as normal. In actual fact this sere occurs only in very sheltered places and is due to local physiographic causes which tend to disappear as the shore line matures. It is exactly comparable with the hydrosere which occurs in ponds and in bays in lakes and is equally limited. On sandy seashores a xerosere occurs, starting with strand vegetation and passing through sand dune and heath to the climax and clearly having no relation to the under-water vegetation. On wave-beaten shores little or no vegetation occurs below water, unless the substratum is rocky, on account of the ease with which sand or mud is moved by waves. On a rocky seashore a succession of communities similar to that already described for a typical lake shore may be postulated, since the upper ones are wave beaten and restricted in number and size of species by this factor, while the lower ones are similarly restricted by low light intensities. It is only in the zone of good illumination and reasonable shelter from water movements that the highest type of community can develop, and owing to the great violence of the waves, the hard substratum and the complicating effect of the tides, this zone is often a narrower one than in lakes.

Owing to the peculiarities of this habitat the succession generally occurs extremely slowly and it may be questioned whether it is legitimate to regard it as a succession at all. It might equally well be regarded as a series of climax communities in different environments. These communities are remarkable in being dominated exclusively by cryptogams. If it is desired to regard the communities as seral the succession could conveniently be called a thalassiosere.

SUMMARY

The chief factors controlling vegetation are considered and the validity of the view that climate is the only one controlling the climax is questioned.

A distinction is drawn between climate and what may be called environmental climate.

The merits of the monoclimax and polyclimax theories are considered; the latter is preferred because it is less likely to obscure facts by over-simplification.

Sere and climax are terms which refer to differences in rate of change, rather than to anything more absolute.

The environmental climate of submerged habitats is characterized in outline, and it is considered useful to distinguish lakes from ponds in a qualitative way by the greater intensity of wave action in the former.

A generalized account of the probable course of evolution of lakes in humid and arid regions is given and it is shown that they present habitats which are probably at least as stable as terrestrial ones.

The plant communities which are found in lakes are therefore best regarded as forming a sere reaching a climax dominated by submerged angiosperms in moderate depths of water where wave action is slight and illumination fairly good.

A brief account of the probable course of this succession is given and the post-climax development of land vegetation in bays is shown to be a true post-climax as it is limited to the original extent of the special conditions.

It is proposed to call the sere in lakes ending in a climax under water a limnosere and to restrict the term hydrosere to the succession in small bodies of water which has a climax on land.

A few examples of hydroseres which have been described from lakes are

examined and are shown to apply only to limited areas in which conditions favour the development of a post-climax.

The normal discontinuity between the vegetation in a lake and that on its shores is pointed out and changes in the vegetation in two senile lakes are summarized.

Habitat conditions in the littoral region of the sea are similar to those in lakes and consideration of marine plant communities agrees with and confirms the position taken up in interpreting lake communities. It is doubtful if a succession in the ordinary sense can be said to occur in the sea.

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THE EXCHANGE OF DISSOLVED SUBSTANCES BETWEEN MUD AND WATER IN LAKES

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(*With forty-six Figures in the Text*)

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Note. Sections III and IV, Summary and References, will appear in the following number of this *Journal.*

INTRODUCTION

GENERAL conclusions of research on the physics and chemistry of lakes during the past forty years have been reviewed by Welch (1935). Water movements induced by wind and the turbulence associated with them are the main agents transporting heat and dissolved substances in lake water. Until density (thermal) stratification is set up by surface warming in the spring, the distribution of heat and dissolved substances, including oxygen absorbed from the atmosphere, is practically uniform from top to bottom. In typical lakes thermal stratification develops during summer, and the zone in free circulation with the atmosphere is confined to a surface layer or *epilimnion.* Below this a narrow zone exists with large temperature gradient (*thermocline*), which offers considerable resistance to wind mixing and separates the epilimnion from the *hypolimnion*. The latter is almost entirely isolated from the atmosphere, and water movement is very much reduced. Thermal stratification is destroyed as a result of surface cooling in the autumn. Decomposition of organic matter, largely derived from dead plankton, depletes the store of oxygen available in the hypolimnion during the development of thermal stratification and at the same time liberates inorganic materials which accumulate in the hypolimnion during the period of stratification. Concurrently plants extract dissolved substances from solution in the epilimnion, which cannot receive much replenishment from below. This depletion of plant nutrients may limit organic production. Circulation between epilimnion and hypolimnion may come too late in the year to revive plant growth; thus the seasonal cycle of thermal and chemical stratification often imposes a seasonal cycle on plant production.

It may be concluded further that the factors controlling organic production in lakes are divisible into two groups, namely, climatic factors, affecting circulation and exchange, and geochemical factors, which include processes both in the lake and its drainage area, controlling the rate of supply of essential nutrients. To complete the causal description of the physico-chemical aspect of organic production in lakes two categories of knowledge are required: first, of the physical and chemical variables which limit plant growth in any specified set of conditions, and second, of the factors controlling the rate of supply of nutrient elements to surface illuminated waters. This paper seeks to supply information on the second category.

Recently, Müller (1938), Einsele & Vetter (1938), and Pearsall & Mortimer (1939) have shown that exhaustion of dissolved oxygen in the hypolimnion during thermal stratification is attended by reduction processes as well as by considerable increases in the concentrations of dissolved substances, including some, e.g. bases, silica and phosphate, which could not be regarded as primary products of reduction. Hence it appears that oxidation-reduction conditions may exercise a profound influence on organic production, not only in determining the free energy of the environment, but also in affecting the rate of supply of nutrients. The work described in this paper is an attempt to gain information on the mechanisms involved in the apparent release of plant nutrients to the water under reducing conditions, by a study of the distribution of physical properties and dissolved substances in lakes which are subject to wide seasonal fluctuations between oxidized and reduced conditions. In base-poor regions, such as the English Lake District, only relatively shallow lakes show complete reduction of oxygen in the hypolimnion. Therefore most of the work was carried out on Esthwaite Water and Blelham Tarn, maximum depth 16 and 15 m. respectively. Observations on mud-water systems in the laboratory and on other lakes in the Lake District are included in §§ II–IV for comparison.

The results have led to the presentation, in outline, of a theory of chemical exchange between mud and water. Deductions from this theory have, as far as possible, been tested on the findings of previous workers. Early in this work, the importance of conditions at the mud surface and in the mud itself was recognized and methods devised for their investigation. The first essential was a sampling device capable of raising an undisturbed sample of the mud surface and the water overlying it. This has been achieved by Mr B. M. Jenkin, whose help I gratefully acknowledge. His apparatus, described in § III, represents an important addition to hydrobiological equipment.

Attention was drawn in a previous communication (Pearsall & Mortimer, 1939) to the correlation of potentials measurable at bright platinum electrodes with chemical evidence of oxidation or reduction in soil and mud-water systems. It was suggested that, although these potentials are not thermodynamically reversible and their interpretation is difficult, they represent oxidation-reduction (*redox*) potentials and are related to ecologically reversible systems. Their practical value lies in the fact that by their measurement it may be determined whether a natural soil or mud-water system is capable of oxidation or reduction. It has been possible to study in detail the redox gradient, which may be confined within the dimensions of a few millimetres near the mud surface. The results go further than the confirmation of the practical value of redox potential measurements; they suggest that the potential itself controls many physical-chemical processes and that the concentration of oxygen, or any other oxidant or reductant, exerts its influence on the system largely through its effect on the potential.

Attention was also directed early in the investigation to the importance of water movements in the transport of physical properties and dissolved substances within the lake system (water and mud), and to the value of the concept 'eddy diffusion', originally applied to problems of meteorology (Schmidt, 1925; G. I. Taylor, 1915), and more recently to oceanography (literature in Defant, 1929). These authors have shown that the laws of diffusion and heat conduction, which have been the subject of detailed mathematical analysis (Carslaw, 1921), also apply to problems of turbulent mixing in fluids. The application to limnology was first attempted by Schmidt (1925). In a future communication (Mortimer, in prep. I) is is hoped to explain more fully the application of certain diffusion integrals to limnological problems.

It was found convenient to present the results of this investigation in three sections, each with a separate description of methods and some discussion. A fourth section—general discussion—follows. For reasons of space, publication of §§ III and IV with summary and references is deferred until the next number of this *Journal*.

I wish to acknowledge the help of Miss W. Pennington with chemical analysis and other measurements on occasions of my absence, and the

painstaking work of G. Thompson and the laboratory staff at Wray Castle in collecting samples. I am indebted to Dr C. B. Taylor for permission to publish the temperature and dissolved oxygen data obtained in connexion with a bacteriological investigation on Esthwaite Water, 1939, and to K. Lee for these determinations.

I. THE DISTRIBUTION OF SOME PHYSICAL VARIABLES AND CONCENTRATIONS OF DISSOLVED SUBSTANCES IN ESTHWAITE WATER, APRIL 1939—FEBRUARY 1940

METHODS

A vertical series of samples was obtained at approximately weekly intervals at a fixed station near the deepest point in the lake (see map, Fig. 1). A Friedinger water sampler was employed and portions of the sample were run off into two 100 c.c. stoppered bottles, taking the usual precautions to exclude air. A third portion of the sample was transferred to screw-cap rectangular bottles of 350 c.c. capacity, of convenient size and shape for packing. Samples were obtained at the following depths: 1, 5, 6, 7, 8, 9, 10, 11, 12 and 13 m.; the last depth was 1 m. above the mud. On each sampling occasion the depth of all samples below 6 m. was adjusted for variations in lake level so that they were at whole-metre intervals above the mud surface. The temperature of the water at these depths was determined at the same time with a reversing thermometer. On some occasions a sample was taken just over the mud surface with an apparatus described in § III. The mud temperatures obtained during 1940 were measured by allowing the thermometer to sink into the soft mud surface, withdrawing it slightly and at the same time reversing it. Evidence from the temperature gradient in the mud investigated by other means indicates that these measurements represent the temperature at approximately 10 cm. below the mud surface.

On return to the laboratory, one of each set of 100 c.c. bottles was used for dissolved oxygen determination (unmodified Winkler), the reagents having been added in the field. The other 100 c.c. bottle was used for the determination of redox potential by the potentiometric method described by Pearsall & Mortimer (1939) and outlined in §§ II and III. A spade-type bright platinum electrode 1 sq. cm. in area was introduced into each bottle, the neck of which was then sealed from the atmosphere by a little medicinal paraffin. The potential was measured 2 hr. after the insertion of the electrodes, which were then cleaned in dichromate-sulphuric acid and well rinsed.

In order to make this chemical survey as extensive as possible, a plan for a selected number of determinations by rapid methods on a large number of samples was adopted in preference to a more complete analysis of a smaller number of samples. Attention was confined to the determination of (*a*) the general characters of the water: electrical conductivity, alkalinity (titration with N 100 HCl to pH 4 with benzene-azo-α-naphthylamine), pH, colour and

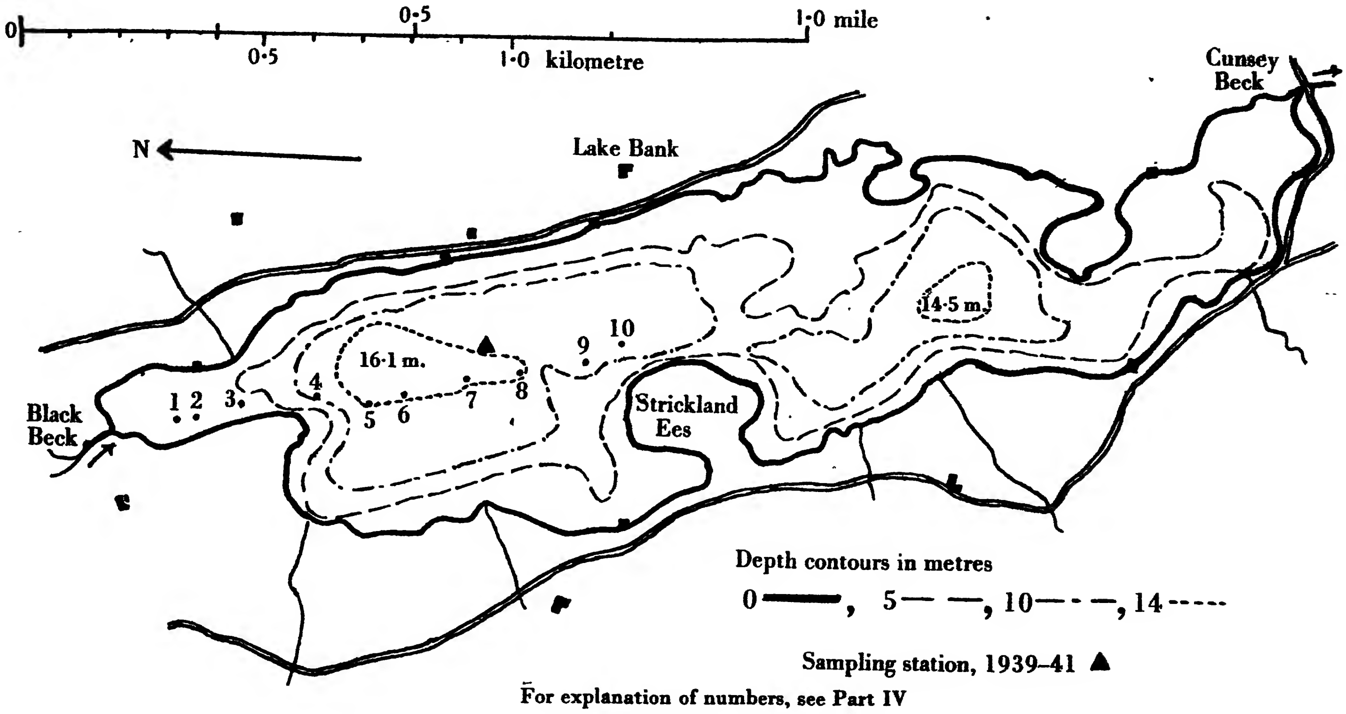


Fig. 1. Bathymetric map of Esthwaite Water. Contours from echo-sounding survey (Mortimer, in prep. VI).

turbidity; (*b*) estimations, on filtered samples, of those substances likely to be involved in redox reactions: ammonia (direct Nesslerization), nitrite (Greiss-Ilsovay), nitrate (phenoldisulphonic acid), manganese (potassium periodate), ferric, ferrous and total iron, sulphide and sulphate; (*c*) other plant nutrients: silicate (ammonium molybdate), phosphate (Denige's method). Brackets indicate standard methods which are described in American Public Health Association (1936). For the following determinations the Lovibond Nesslerizer with coloured glass standards was used and effected a considerable saving in time—ammonia, nitrite, silicate, phosphate and *p*H. The silicate disk was calibrated for nitrate estimation, as the yellow tint produced in both determinations is identical. Difficulty was experienced in nitrate estimation in waters containing considerable dissolved organic matter, due to disturbing brown colourations produced with the acid. This disturbance was minimized when ammonia was employed for neutralization and in most cases the brown tint could be distinguished from the picric acid yellow, especially as the latter developed more rapidly after neutralization.

Fuller descriptions of non-standard methods will be given elsewhere. Colour was determined in arbitrary units using the ammonia standard disk of the Lovibond Nesslerizer, the tint being very similar to water colour. 'Turbidity' or 'transparency' was determined by means of a photo-electric photometer designed for the purpose (Mortimer, in prep. II). The total transmission of white light through a column of the sample (350 c.c.) was measured and expressed as a percentage of transmission through distilled water, measured under identical conditions. This result included absorption due to turbidity and colour. A correction for the latter may be made by a transparency determination on a filtered sample.

An instrument has been designed (Mortimer, in prep. III) to determine the electrical conductivity of water and mud samples with a d.c. galvanometer and to correct the readings to 18° C. Before passing to the electrodes the d.c. was converted into a.c. by means of a commutator driven by a gramophone motor. The electrodes, which consisted of two sheets of bright platinum, total area approximately 1 sq. cm. wrapped round and fused to a glass tube (Fig. 16), were sufficiently robust to be lowered into mud cores without damage. This instrument, which may also be used in the field, possesses certain advantages for the rapid evaluation of conductivity and the study of its distribution in undisturbed mud-water systems. Expressed as reciprocal megohms at 18° C. ($K_{18} \times 10^{-6}$), the conductivity value may be taken to be almost exactly 1·6 times the total concentration of dissolved salts in waters in which bicarbonate is the main anion (Kitto, 1938).

Tests for free ferric iron with potassium thiocyanate were invariably negative, although ferric ions appeared in many cases after treatment with acid, which probably released them from a ferric-organic or similar complex. 'Ferrous iron' was estimated by the increase in colour with potassium thiocyanate after oxidation of the sample with hydrogen peroxide (one drop of Perhydrol, Merck). 'Ferrous iron' was also detected with α-α'-dipyridyl. From the conclusions of Cooper (1937) and the findings of Coolidge (1932) it is clear that much of the ferrous iron must have been in complex form at the *p*H of the Esthwaite samples. Total iron was estimated with potassium thiocyanate after preliminary digestion of 50 c.c. sample (less in samples with high iron concentration) with 0·5 c.c. concentrated nitric acid, A.R.

Perhaps the most sensitive test for hydrogen sulphide is smell. Although traces of H_2S were detected in this way in some samples, no sulphide could be detected with cadmium sulphate by the method described by Ohle (1936*a*). It is probable that in the presence of free ferrous ions at the *p*H of the water concerned almost all sulphide was precipitated as ferrous sulphide.

Hitherto the determination of sulphate in waters with low concentration of this ion has been a tedious matter. Nevertheless, estimation of sulphate is necessary for a study of redox reactions in natural waters. During the course of this investigation a conductimetric method was developed (Mortimer, in prep. IV). 25 c.c. of sample, to which an equal volume of ethyl alcohol had been added, was titrated against standard barium chloride. The rate of change of conductivity, measured during the titration by means of the instrument already described, exhibited a sharp discontinuity at the end-point. By this method the low concentrations of sulphate encountered in the waters investigated (0–10 mg./l. SO_4) could be estimated to within 0·2 mg./l. SO_4. A single determination took about 5 min.

Note on the presentation of results. The usual practice of representing thermal or chemical stratification by a series of vertical distribution graphs becomes impracticable when detailed results for frequent time and depth intervals are presented. One method, adopted by Birge & Juday (1911), is to plot the value of the physical variable or concentration on the ordinate, and time along the axis, and then to join the plotted values for each depth by a single line labelled for that depth. Another method employed here (cf. Yoshimura, 1936*a*), offers certain advantages. As before, time is plotted along the axis, but the ordinate is depth in metres. The diagram thus represents a depth-time chart, and a separate one is prepared for each investigated property of the water. The value of this property in each sample is written on the diagram at the appropriate depth and time. Isotherms or isopleths (lines of equal concentration) are then drawn freehand by inspection. In this way tables have been eliminated and the diagram provides a picture of the development of vertical distribution with time. With practice, detailed interpretation of the diagram becomes easy. Thus isotherms or isopleths bunched together at one depth indicate marked vertical stratification at that depth; changes in slope of the lines may indicate mixing from above or below, and vertical lines show uniform distribution throughout the water column.

RESULTS

Only a selection of the results can be presented here and only some of the conclusions can be indicated in the text. Further interpretation of the depth-time diagrams is left to the reader. The full data may be inspected at Wray Castle.

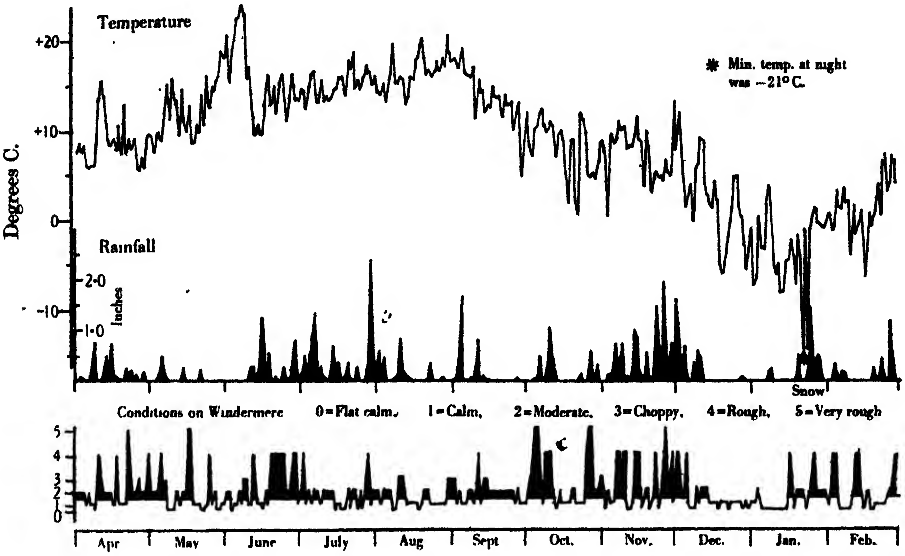


Fig. 2. Meteorological records, 1939–40; air temperature (9 a.m. Ambleside), rainfall (daily totals Ambleside) and observations on Windermere (estimate of mean daily condition).

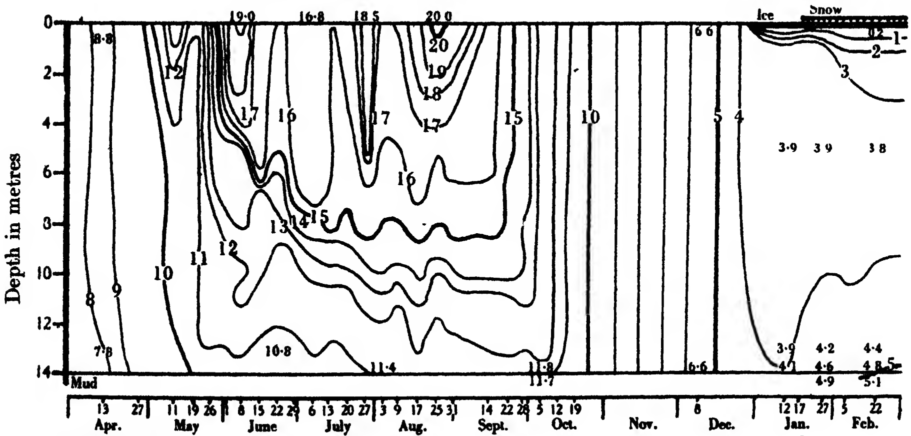
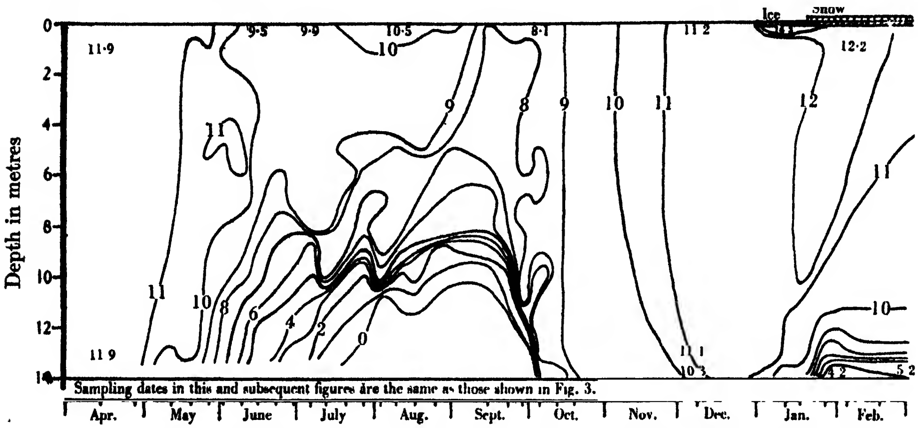


Fig. 3. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of temperature (° C.).

Weather, lake temperature and dissolved oxygen. The influence of weather on lake temperature is clear from a comparison of Figs. 2 and 3. Data for wind are clearly inadequate. Daily observations of conditions on Windermere do not necessarily hold for Esthwaite Water 3 miles away, but the major oscillations in wind force may be considered to apply equally to both lakes.

The main features of the temperature cycle were as follows: Isothermal conditions continued into April. Thermal stratification commenced at the beginning of May, was destroyed by a gale in the middle of that month, but was re-established during the calm warm spell that followed. The epilimnion was deepened by rough weather at the end of June, the thermocline was pushed down to about 8 m. and throughout the summer was not very narrowly defined. Stability, i.e. thermal resistance to wind mixing, was highest between 8 and 12 m. As a result of surface cooling during September the epilimnion was progressively deepened until gales in the beginning of October re-established complete circulation.



Sampling dates in this and subsequent figures are the same as those shown in Fig. 3.

Note. Determinations by Winkler procedure with no preliminary oxidation of reducing substances.

Fig. 4. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of dissolved oxygen (mg./l.).

As soon as thermal stratification was established the concentration of dissolved oxygen below the thermocline began to fall (Fig. 4). The rate of fall at each level was progressively greater as depth increased. By methods illustrated in a later communication (Mortimer, in prep. I) it has been deduced that most of the oxygen absorption took place at the mud surface. Oxygen was completely consumed (unmodified Winkler determinations) in the lowest sample by the end of July. After this the de-oxygenated zone increased in height to above the 11 m. level in September, but was progressively destroyed by mixing with oxygenated water from above at the end of that month, finally disappearing at the overturn on 5 October. The high concentrations found at the surface during the summer represented percentage saturation values of over 100 at the temperatures concerned, produced in part at least by the photosynthetic activity of phytoplankton.

The increase in oxygen concentration throughout the whole lake during the early winter was a result of the greater absorption capacity of the water as the temperature fell. The concentrations found represent percentage saturation values varying between 90 and 95. The decrease in concentration in surface layers during September may be considered to have been the result of the progressive mixing of these layers with de-oxygenated hypolimnion water as the level of the thermocline fell. The high concentrations of iron encountered in the surface waters during the same period (Fig. 6) indicates that the substances which absorbed oxygen were associated with iron, which did not disappear from these waters until some months later. As inorganic iron is practically insoluble in oxygenated neutral or alkaline water, it must be supposed that the relatively high concentrations in surface waters were present either as colloidal ferric hydroxide or as soluble or colloidal ferric-organic complexes, probably similar to those formed in waters and soils in the presence of humus. Such colloids or even floccs would be kept in suspension by wind circulation, and the sharp fall in concentration which occurred under ice (Fig. 6) may be interpreted as the result of settling of these materials. In any case the mechanism is of interest in suggesting the manner in which iron may be supplied to the phytoplankton (cf. Hutchinson, 1941).

Redox potential and iron. As a result of the insolubility of ferric iron in most natural waters, the concentration of iron remained low in all samples from Esthwaite Water in which the oxygen concentration had not fallen below a certain level, say 5 mg./l. The mud, however, in common with most lake muds, is anaerobic just below the surface and contains ferrous iron, which is soluble. It must therefore be assumed, and observation has confirmed the assumption, that ferrous iron cannot penetrate into oxygenated water, but is precipitated in ferric form on the mud surface (Einsele, 1938; Pearsall & Mortimer, 1939). High concentrations of iron in the water are only maintained in the absence of oxygen. That high concentrations occur in the de-oxygenated hypolimnion of lakes has been observed by various workers (Müller, 1938; Einsele, 1938; Yoshimura, 1936*b*; Stangenberg, 1936; Pearsall & Mortimer, 1939). The latter authors found that ferrous iron appeared in the water of Blelham Tarn, and also in soils and muds, only if the redox potential fell below $E_7 = 0{\cdot}23$ V., which corresponded in Blelham Tarn to an oxygen concentration of about 0·5 mg./l.

The controlling influence of the concentration of dissolved oxygen on the distribution of redox potential and iron and of other dissolved substances in Esthwaite Water (1939) is demonstrated by the similar course of the isopleths in Figs. 4–6 and subsequent diagrams. After thermal stratification had commenced, the rise in concentration of iron in the bottom sample was relatively slow until the dissolved oxygen concentration had fallen to about 1 mg./l. in the middle of July. At this time the iron concentration in the bottom sample was 0·75 mg./l., and the redox potential had only fallen approximately 0·1 V.

from the value usually found in well-oxygenated water ($E_7 = 0{\cdot}5$ V.). From this point onwards the rise in total iron concentration was more rapid. It trebled in a fortnight and the potential fell to 0·25 V. As yet no ferrous iron had appeared in the bottom sample. It must therefore be assumed that the increase in iron resulted from increased diffusion of ferrous iron from the mud

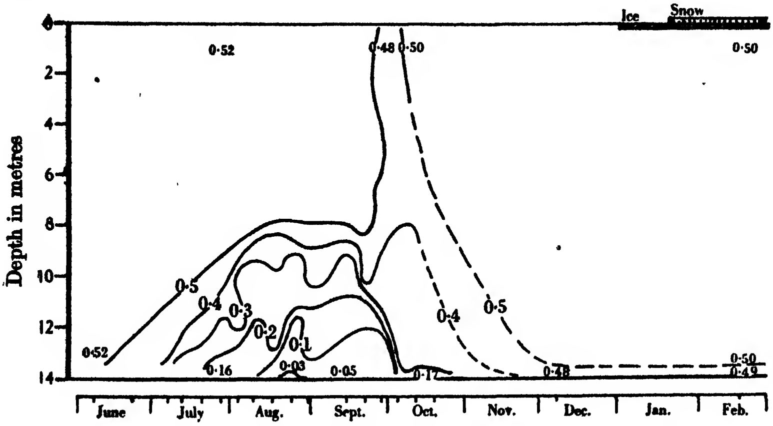
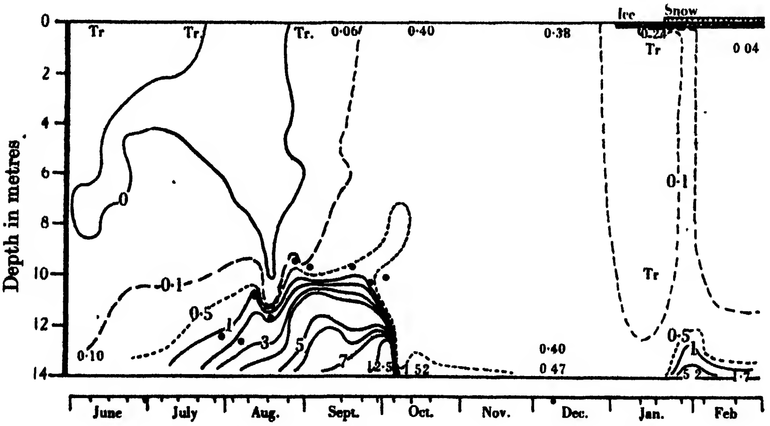


Fig. 5. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of redox potential (E_7 in V.).



● = Highest level at which ferrous iron was detected.

Fig. 6. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of total and 'ferrous iron' (mg./l. Fe).

at lower oxygen concentrations near the mud surface, and its oxidation at higher levels. As a result of this the water became cloudy and coloured with ferric hydroxide. Free ferrous iron first appeared in the bottom sample on 27 July, when the oxygen had disappeared and the potential had fallen to $E_7 = 0{\cdot}18$ V. The rapid rise in iron concentration was maintained throughout the summer, reaching a maximum value in the bottom sample of 12·5 mg./l. on 28 September, by which date the potential had fallen to $E_7 = 0{\cdot}05$ V.

For reasons of space, data for ferrous iron are included on the total iron diagram (Fig. 6). As the summer proceeded it made up a progressively increasing part of the total iron in the hypolimnion (see Fig. 11) until on 28 September all the iron in the bottom sample was in the ferrous or ferrous complex state. The persistence at other levels of the de-oxygenated zone of some iron not in 'ferrous' form may have resulted from the presence of unionized ferrous complexes or from the slow rate of reduction of ferric complexes produced from the large-scale oxidation of ferrous iron during July and from the continuous oxidation and precipitation of iron, which may be expected to occur at the thermocline level. A turbidity maximum (cf. Fig. 11) indicated that oxidation of iron was in fact proceeding in the upper layers of the hypolimnion. These layers were considerably more turbid than the bottom water, which became clearer but more coloured as the summer proceeded. Possible accumulation of plankton at the thermocline level should also be borne in mind. The upper limits of occurrence of ferrous iron coincided with an oxygen concentration of approximately 0·5 mg./l. and a potential of approximately $E_7 = 0{\cdot}25$ V. An exception to this rule occurred during unstable conditions resulting from active mixing in the 10–13 m. layer on 28 September, a few days before the overturn. Ferrous iron was detected at 10 m. at a potential of 0·37 V. and oxygen concentration of 8·4 mg./l.

The restoration of dissolved oxygen to the mud surface at the overturn effected a rapid oxidation and precipitation of the iron, most of which was deposited on the mud surface (see Fig. 12). Nevertheless, as was pointed out earlier, the iron concentration in the whole lake remained relatively high during the early part of the winter. A sharp rise in redox potential was observed at the time of oxidation and precipitation of the iron, although the high spring values were not equalled until about 2 months later. These values are comparable with those obtained in oxygenated sea water (Cooper, 1938) and oxygenated distilled water (Richards, 1928) if corrections are made for *p*H value. The fact that these potentials were not attained until December may be considered as further evidence that reducing materials were present in the water during the preceding months.

Colour. The time-depth distribution of colour is not figured. Colour was negligible in surface waters. In the hypolimnion it was partly due on some occasions to the presence of colloidal ferric hydroxide and partly to coloured soluble organic substances diffusing out of the mud. Colour due to this latter cause increased in the hypolimnion to a maximum just above the mud at the end of the stagnation period. After the overturn it was decreased to less than one-tenth of this value. A typical vertical distribution of colour during summer stratification is shown in Fig. 11, and a graph showing the seasonal variation of the 'total colour' in the water column is included in Fig. 13.

From the sharp fall in total colour at the overturn it is apparent that much of the soluble organic matter is removed at the same time as iron.

Silica (Fig. 10) also showed a progressive increase in concentration from 1 to over 3 mg./l. SiO_2 in the hypolimnion during the course of the summer. The mean concentration after the overturn was 2·0 mg./l. This represents a slight decrease in mean concentration of silica in the whole water column of 0·1 mg. as a result of the overturn. The corresponding decrease during 1940 was greater (Fig. 12). This point is discussed later.

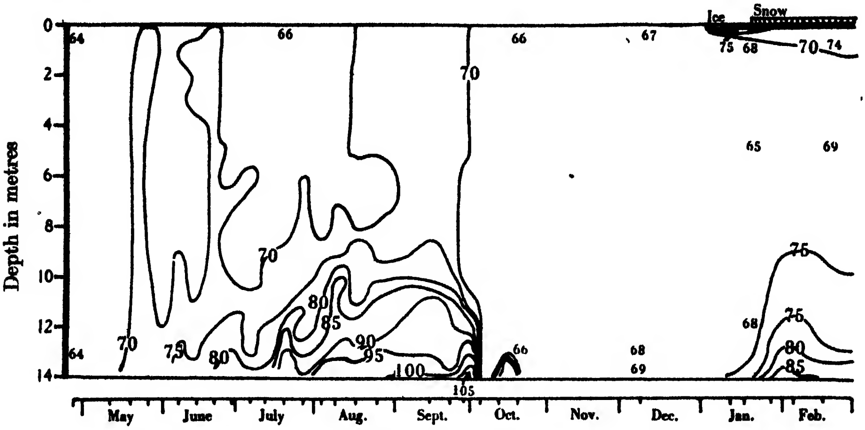


Fig. 7. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of electrical conductivity ($K_{18} \times 10^{-6}$).

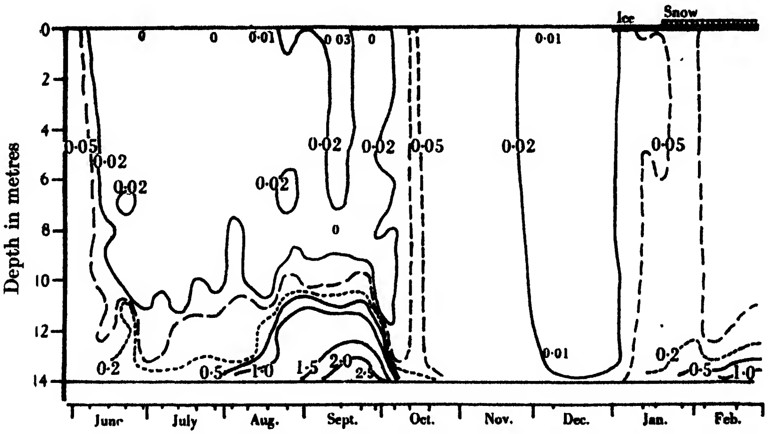


Fig. 8. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of ammonia (mg./l. NH_3.N).

Electrical conductivity (× 0·63 = total dissolved salts; cf. Kitto 1938) rose at the mud surface from about 70 at the beginning of June to 109 on 28 September. This corresponds to an increase in total dissolved salts of approximately 60 mg./l. It is shown in later discussion that this increase can be accounted for by the observed increases in iron, ammonia and other bases. At the overturn there was a sharp fall in the mean conductivity of the whole water column from 76 to 67, a decrease of 12 %. It is suggested in later discussion that this amount must have been absorbed by the mud, as the period

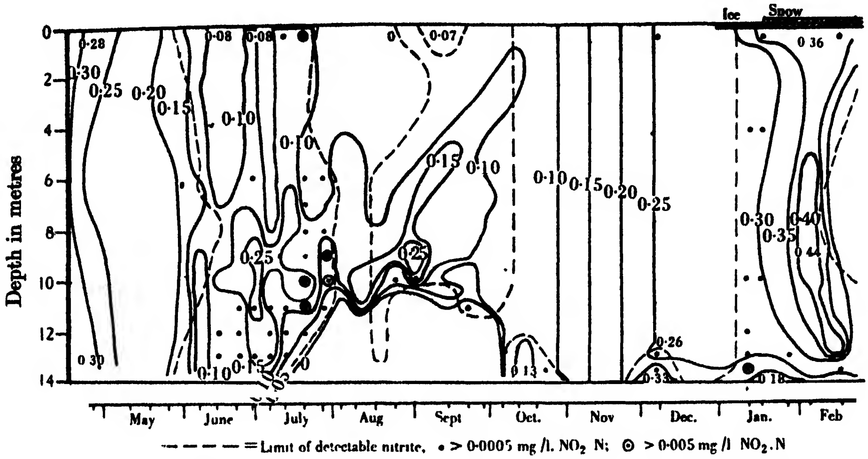


Fig. 9. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of nitrate ($NO_3.N$) and nitrite ($NO_2.N$).

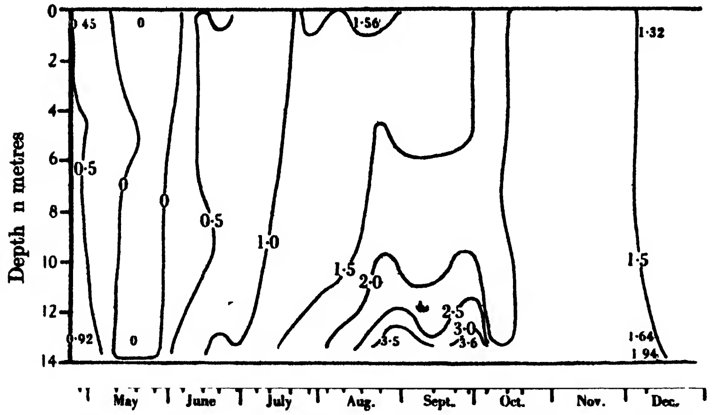


Fig. 10. Esthwaite Water, 1939–40. Depth-time diagram of the distribution of silicate (SiO_2).

between 28 September and 5 October was not long enough for any change in the conductivity of the inflow water to have caused this decrease.

Ammonia, nitrite and nitrate (Figs. 8, 9, 11). The rise in ammonia concentration in the hypolimnion followed a similar course to that of iron, although it began somewhat earlier, reaching a maximum of 2·6 mg./l. $NH_3.N$ just above the mud surface on 22 September. In the epilimnion, and in the whole lake

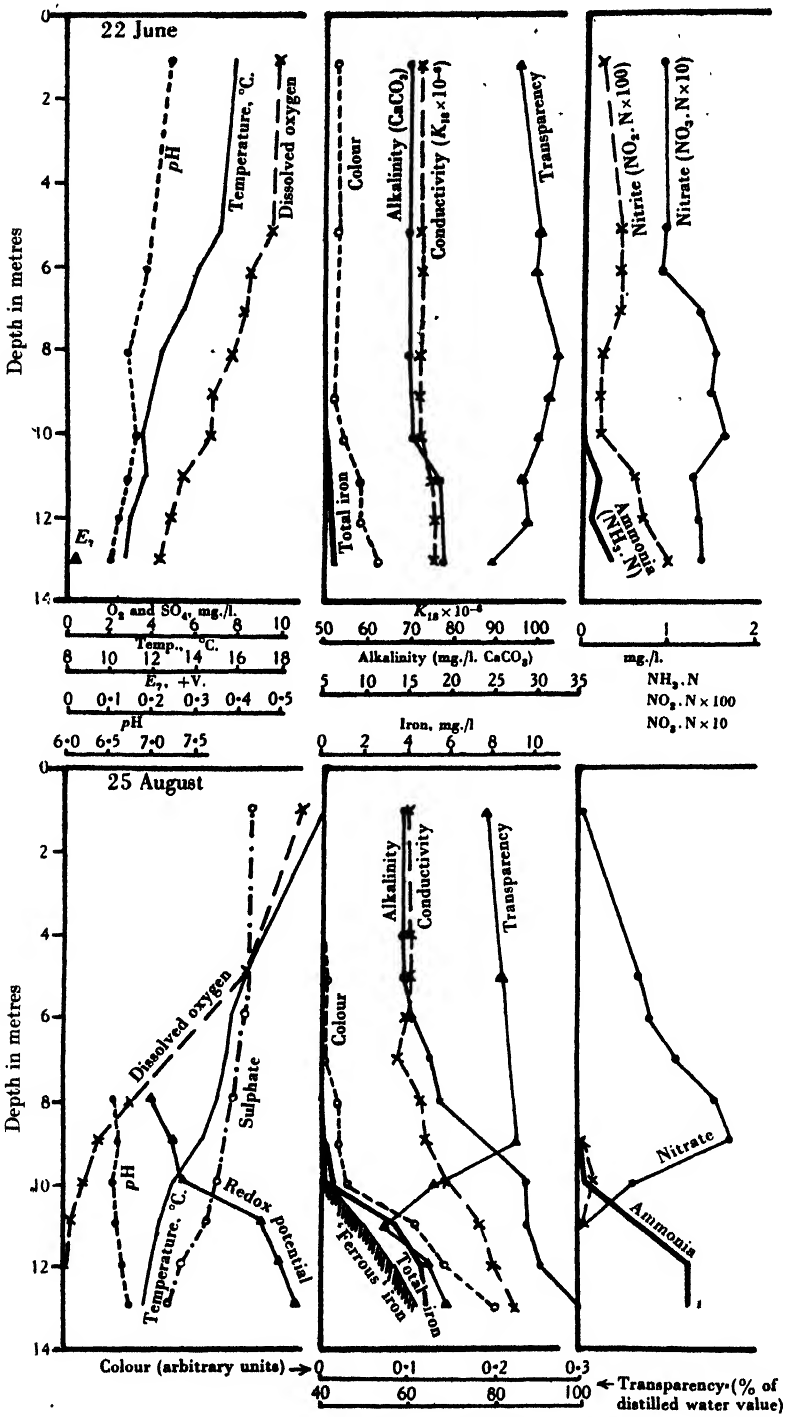


Fig. 11. Esthwaite Water, 1939. Vertical distribution of some physical variables and concentrations of dissolved substances at four weeks (22 June) and thirteen weeks (25 August) after the establishment of thermal stratification.

after the overturn, the ammonia concentration was normally about 1/100 of this value. It will be seen that the increase in ammonia was about ten times the equivalent amount of nitrate reduced in the hypolimnion. This point will be discussed later. The nitrate diagram shows that rapid reduction of nitrate occurred in the hypolimnion when the oxygen concentration and the redox potential had fallen below approximately 2 mg./l. and $E_7 = 0{\cdot}4$ V. respectively. Depletion of nitrate also occurred in the epilimnion. This may be mainly due to assimilation by algae. Hence the highest concentrations were found in the thermocline region, where a slow increase during August was observed. There was a steady increase in the nitrate content of the whole water column during the early winter, although a lag of about 1 month intervened between the overturn and the commencement of this increase. Thus on 28 September the mean concentration ($NO_3.N$) throughout the whole water column was 0·068 mg./l. and by 19 October it had only risen to 0·079.

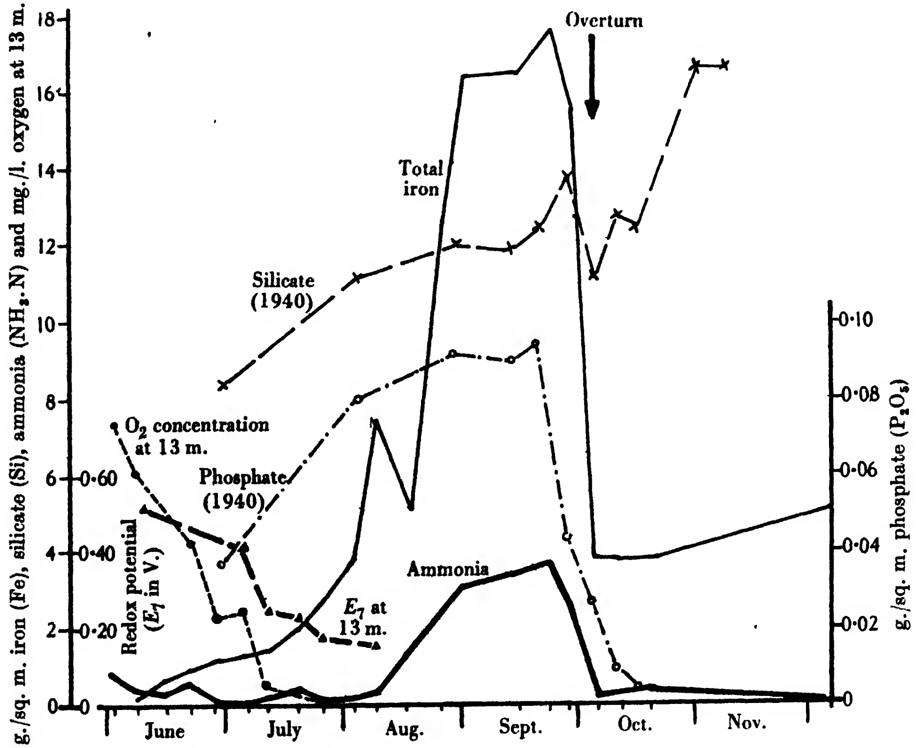


Fig. 12. Esthwaite Water, 1939 and 1940. Variation in total content of iron and ammonia (1939), silicate and phosphate (1940), in the water column (0–13 m.) above 1 sq. m. of mud surface at the sampling station. This is compared with the oxygen concentration and redox potential in the lowest sample (13 m.).

Data for nitrite have been included on the nitrate diagram. Nitrite was only found in very small concentrations and, as the diagram shows, the greatest amounts were found in the thermocline region, usually a metre or so above that level at which nitrate was completely reduced and a rise in ammonia concentration observed. This supports the view, expressed by Pearsall & Mortimer (1939), that the main source of nitrite is nitrate reduction and not ammonia oxidation. Experiments, mentioned later in discussion, have shown that little oxidation of ammonia takes place in the water. Nitrite was absent from the fully reduced hypolimnion, but traces were often found in surface waters. These may have been associated with the activities of the phytoplankton.

Sulphate and sulphide. The conductometric method of sulphate estimation was not developed until the summer of 1939, and the data presented here for that year are confined to a typical vertical distribution during August (Fig. 11). Sulphate became progressively depleted in the hypolimnion during the course of the summer. The lowest concentration recorded was 2·6 mg./l. SO_4 just over the mud surface on 28 September. The concentration throughout the whole water column rose almost immediately after the overturn to the winter value of about 9 mg./l. SO_4. More complete data for sulphate are presented in § III. In a later communication (Mortimer, in prep. I) it will be demonstrated that depletion of sulphate in the hypolimnion of Esthwaite Water, 1940 can be accounted for by reduction at the mud surface, and that reduction in the water was negligible. Neither during 1939 nor during 1940 was the sulphate in the hypolimnion completely reduced.

Concentrations of soluble sulphides in the hypolimnion were too small to be estimated by standard methods, although H_2S was detected by smell in the lowest samples during August and September, and black cloudiness due to colloidal ferrous sulphide appeared in the lower hypolimnion during the latter month. Production of ferrous sulphide in the water was not observed during 1940. The pH of the lower hypolimnion during September was about 6·9. As a result of the extremely low solubility coefficient of ferrous sulphide at this pH, almost complete removal of sulphide ions from solution occurs in the presence of ferrous ions (cf. Einsele, 1937). This probably explains why no soluble sulphide could be detected.

Alkalinity and pH. A progressive rise in alkalinity occurred in the hypolimnion during stagnation. The course of this rise and of the corresponding fall after the overturn was similar in almost every detail to that already described for conductivity. Hence a time-depth diagram for alkalinity is omitted. The relation of alkalinity and conductivity is discussed later. In the absence of free mineral or organic acids, pH depends on the relative concentrations of free carbon dioxide and alkalinity. In fact, if any two members of this triple relation are known, the third may be computed (convenient graphs in Moore, 1939). Thus it would be possible to compute the concentration of dissolved CO_2 in Esthwaite Water from the pH and alkalinity values found. This has not been done, as the results of direct CO_2 determinations are described in

§ III. It will be shown there that the rate of CO_2 production in the hypolimnion was high while the dissolved O_2 was being reduced, but that little anaerobic CO_2 production took place subsequently. This explains why, during 1939, the *p*H at 13 m. was observed to fall from 6·9 to 6·5 during June, as a result of CO_2 accumulation in the hypolimnion. Later, as the alkalinity increased, the *p*H at 13 m. rose to 6·9 at the end of September. This difference in the vertical distribution of *p*H at the beginning and towards the end of stagnation is illustrated in Fig. 11.

Phosphate. Estimations of phosphate were only carried out on a few samples from Esthwaite Water during 1939. Distribution of phosphate was studied in more detail during 1940 and discussion is deferred until § III. During both years the phosphate concentration in the hypolimnion rose from the extremely low values prevalent in oxygenated water (about 0·001 mg./l. P) to over a hundred times this concentration in de-oxygenated layers. This agrees with previous findings (Pearsall & Mortimer, 1939) and with the explanation advanced by Einsele (1938). He showed that under oxidizing conditions phosphate is precipitated in the presence of iron as insoluble ferric phosphate on the mud surface. When this is reduced, soluble phosphate is liberated.

Manganese. Discussion of the distribution of manganese is postponed until § III.

DISCUSSION

(*a*) *Deductions from the distribution of temperature and dissolved substances in the hypolimnion*

The course of the isopleths in Figs. 4–10, and indeed the fact that vertical chemical stratification is maintained in the water column, suggests that the main agents of production or depletion of dissolved substances are located at the lower boundary of the column, at the mud surface. If the water were completely stagnant, i.e. in the absence of motion of water masses, transport of dissolved substances to and from the mud surface would be the result of molecular diffusion, the laws of which can be deduced from consideration of the random movements of molecules (Mortimer, in prep. I). In lakes this mode of transport is confined to the water within the interstices of the mud. In the water above the mud some motion of water masses occurs under almost all natural conditions, and it may be demonstrated that even the slowest of these movements, e.g. convection currents under ice, produces turbulent eddies which are instrumental in spreading heat, dissolved substances or other properties in the water. In a water column, of sufficient magnitude compared with the mean diameter of the eddies, the spread of a property by 'turbulent' or 'eddy diffusion', considered over a period sufficiently long to average out short-term fluctuations, approximates to that produced by random motion. In other words the laws of diffusion and heat conduction may be directly applied (Schmidt, 1925). The fundamental assumption, verified by experiment, at the basis of these laws is that the amount (F) of substance or heat, etc., passing across a boundary of unit area in unit time is the product of the appropriate coefficient of conduction or diffusion (K) and the gradient of temperature, concentration, etc., existing at the boundary along an axis normal to it. Thus considering diffusion of a dissolved substance and employing c.g.s. notation:

$$\text{Amount in grams diffusing across 1 sq. cm.} = Ft = Kt\ (\text{gradient, g./cm.}), \qquad (1)$$

where t is the duration of the period in seconds and K may either be the coefficient of molecular diffusion or the coefficient of turbulent diffusion. Following Schmidt (1925) the letter A is employed for the latter ($A=$ 'Austauschkoeffizient') to distinguish it from K, the coefficient of molecular diffusion.

Changes in the vertical distribution of dissolved substances and temperature may, in favourable instances, be used in conjunction with formula (1) to obtain an estimate of A. The method at the basis of all such estimations in this paper is illustrated by the following calculation of a mean value of A at the 12 m. level in Esthwaite Water during the period 27 July to 31 August 1939. Data for total iron were utilized and c.g.s. notation was employed throughout. This period was selected as one during which free exchange of iron between mud and water occurred (see later discussion) and because the increase in the iron content of the water column above 12 m. during the period was considerable. As the mud was the only source of iron, this increase ($6{\cdot}4 \times 10^{-4}$ g./sq. cm., obtained by summing the mean iron content of each metre panel above 12 m.) must have been transported up through the 12 m. level by eddy diffusion. The mean concentration gradient at this level may be taken as roughly the mean of the differences in concentration between 11 and 12 m. and 12 and 13 m. on all the sampling dates during the period, and was computed as 0·84 mg./l./m. or $8{\cdot}4 \times 10^{-9}$ g./c.c./cm. Substituting in formula (1), where $86{\cdot}4 \times 10^{3}$ is the number of seconds in a day and 34 days the length of the period,

$$A = \frac{6{\cdot}4 \times 10^{-4}}{8{\cdot}4 \times 10^{-9} \times 34 \times 86{\cdot}4 \times 10^{3}} = 2{\cdot}6 \times 10^{-2}.$$

Similar estimates can be made in all cases in which it is certain that *all* of the increase in heat or concentration of dissolved substance on one side of the level investigated has been derived from the other side by diffusion, and as long as the stratification of temperature or concentration in the region of that level is large enough to enable reliable estimates of the gradient to be made. In favourable cases a rough estimate of A can be made more rapidly from the spacing and slope of the isotherms or isopleths on a depth-time diagram. Values of A, or more strictly speaking $A+K$, at various levels in the hypolimnion of Esthwaite Water, estimated as above from the distribution of various properties, are collected in Table 1. Values for Schleinsee were estimated from data obtained by inspection of Einsele & Vetter's (1938) diagrams and are included here for comparison.

Estimations of A during stagnation under ice are presented later in Table 2. It will be seen in Table 1 that estimates of A, obtained from the consideration of heat passing down through lower levels of the hypolimnion, are consistently lower than those obtained from the upward spread of dissolved substances. As there is good agreement between estimates of the latter class, it is likely that the low values obtained from temperature distribution resulted from the failure to account for heat passing into the mud (cf. Birge *et al.* 1928). The discrepancy disappears when the upward flow of heat under ice is considered (Table 2). It should be emphasized that the data only permit approximations to the mean value of A at a certain level and for a certain period to be made. The agreement between estimates derived from different data indicates, as would be expected, that A is the same if computed from any conservative property of the water; it is solely an index of the rate of exchange of the water masses bearing these properties. The value 3×10^{-2} may therefore be taken as a rough estimate of A in the lower hypolimnion during summer stratification. It may be an under-estimate, as the above calculations have taken no account of salts diffusing through the thermocline and lost at the outflow. The value of these estimates lies in the fact that they demonstrate that water movement and eddy diffusion continue in the hypolimnion after thermal stratification has become established, for they yield a value of A which is over 20 times as great as the corresponding coefficient of molecular heat conduction, and approximately 2000 times as great as the coefficient of molecular diffusion

Table 1. *Estimates of the eddy diffusion coefficient* ($A \times 100$) *at various levels in the hypolimnion of Schleinsee and Esthwaite Water*

Lake	Esthwaite Water							Schleinsee	
Depth of bottom at sampling station (m.)	14·0							11·6	
Year	1939						1940	1935	
Period	8. vi.–29. vi.*			27. vii.–29. viii.			3. viii.–29. viii.	15. iv.–24. v.	24. v.–6. viii.
Lower limit of thermocline (m.)	7			10			9	—	7
Depth of estimation (m.) ...	13	12	10	13	12	10 = thermocline	13	11	11
	Mean values of $A \times 100$ for period								
Data employed:									
Ammonia	—	—	—	—	—	—	—	2·5	1·5
Total iron	4	3	3	2·8	2·6	—	3·8	—	1·8
Conductivity	4	3	2	2·6	3·3	1·0	3·6	—	—
Phosphate	—	—	—	—	—	—	—	—	1·6
Sulphate	—	—	—	—	—	—	3·7	—	—
Temperature	—	—	—	—	2·3	0·8	1·8 (12 m.)	—	1·0

* Data during this period only allow the order of magnitude of A to be roughly estimated. Estimations during other periods may only be considered significant to one figure. The second figure is included in this table and in Table 2 to demonstrate the magnitude of differences between estimates derived from different data.

of most common solutes. This considerable difference between the rate of transport of substances in the mud, where molecular diffusion alone is operative, and in the water, even under conditions of thermal stratification, explains many of the phenomena described and discussed later.

The above calculations should not, however, give the impression that A is at all constant in value at any point for the whole of the periods investigated. It will be suggested later in § IV that water movements in the hypolimnion result from wind-induced instability in the thermocline region. Although there is not space here to demonstrate the relation of weather and the magnitude of A in the hypolimnion, an inspection of the course of the isotherms and isopleths on the depth-time diagrams will show that considerable variations occur and that these are associated with variations in wind force. Examples of this may be found in the increase in slope of the oxygen isopleths indicating increased mixing in the central hypolimnion (11–12 m.) at the end of June 1939, and a similar increase in slope of the isotherms at the end of August 1940, both as a result of rough weather. Neither should it be assumed that A has the same value at all levels of the hypolimnion. It is to be expected that A is considerably reduced in regions of considerable thermal (density) stratification, as turbulent exchange in such regions also involves work against gravity. The results of attempts to determine the magnitude of A in the thermocline region, on somewhat inadequate data, are included in Table 1. The low values found illustrate the effect of the thermocline in isolating the hypolimnion from the epilimnion. In the epilimnion and in the whole lake during winter circulation A may be several hundred times as great as in the hypolimnion (Schmidt, 1925). It will, of course, fluctuate in value considerably with varying wind force. A direct result of the occurrence of these high A values is the virtual disappearance of detectable concentration or temperature gradients in the water. A consideration of formula (1) will show that, if the rate of supply of heat or a solute at a terminal boundary of the water column (i.e. lake surface or mud surface) varies only within fairly narrow limits, the concentration gradient must vary inversely as A, which clearly varies enormously at different levels and seasons. In the mud, on the other hand, where the exchange coefficient is reduced to that of molecular diffusion, steep concentration gradients are found to be compressed into the dimensions of a few millimetres ('microstratification', Alsterberg, 1927, 1930), cf. § III.

The distribution and transport of properties in the lake system will be considered in more detail in a later communication (Mortimer, in prep. I). By means of the application of methods of mathematical physics it is possible to assess the relative influence of reactions in the mud and in the water on changes in the distribution of dissolved substances in the mud-water system. The conclusions reached are that reactions in the mud are largely responsible for changes in distribution in the water; movement of water masses in the hypolimnion is mainly horizontal and this is sufficient to maintain an eddy diffusion coefficient and a rate of spread of dissolved substances roughly two thousand times as great as would occur if molecular diffusion alone were operative. How these water movements may be produced is discussed later.

(b) *Seasonal variations in the rate of exchange of dissolved substances between mud and water*

In Fig. 12 variations in total content of certain dissolved substances in the water column of 1 sq. m. cross-section, extending from 13 m. to the surface, are plotted for Esthwaite Water, 1939. If these are compared with the dissolved oxygen concentration and redox potential in the lowest sample (13 m.), certain correlations become apparent.

Only the more striking changes may be correlated with redox conditions in the hypolimnion, as the effect of slow changes resulting from variations in composition of inflow water has not been considered. The sequence of events may be described as follows: Removal of oxygen from the hypolimnion (see Fig. 13) commenced as soon as thermal stratification was established. The depletion rate was fairly constant during the initial stage, but became less at the point when the oxygen concentration in the bottom sample had fallen to about 2 mg./l. This reduction in depletion rate may have been the result of a corresponding decrease in the concentration gradient at the mud surface. Up to this time (stage I), alkalinity, iron and colour had increased slightly. The next stage (II), during which the oxygen concentration and redox potential at 13 m. fell to 0·5 mg./l. and $E_7 = 0{\cdot}25$ V. respectively, was marked by an acceleration in oxygen depletion rate (Fig. 13) and the beginning of a sharp rise in the content of iron, and an increased rate of accumulation of 'total salts' (conductivity × 0·63; cf. Kitto, 1938), alkalinity and colour (Figs. 12–14). Turbidity also increased during stage II. From the data for phosphate and silicate for Esthwaite Water, 1940 (included in Fig. 12, because they are more complete than data for 1939) it may be assumed that stage II also marks the beginning of a rise in silicate and a considerable rise in phosphate content.

It is suggested here and proved in later sections that stage II is initiated by a fall in oxygen concentration and redox potential at the mud surface to a level at which oxidized insoluble ferric substances including ferric phosphate are reduced in the mud surface. This liberates soluble ferrous iron and probably other reducing substances into the water. As long as the potential at the mud surface is maintained below this level, i.e. until the autumn overturn, diffusion of ferrous iron, phosphate, etc., from mud into the water continues. It has been shown earlier that the rate of spread of these reducing substances was increased roughly 2000 times as soon as they left the mud and came under the influence of eddy diffusion in the water. The acceleration in the oxygen depletion rate between 6 and 13 July, was probably a direct result of this liberation and accelerated spread of ferrous iron and other reducing substances into the water. The oxygen concentration and redox potential at 13 m. fell during this period from 2·5 to 0·5 mg./l. and from 0·42 to 0·25 V. respectively. It is probable that the corresponding values at the mud surface (14 m.) were lower at this time.

The oxidation of this ferrous iron produced a marked increase in turbidity and colour due to the precipitation of ferric hydroxide in colloidal or finely suspended state. Free ferrous iron was not detected in the water in amounts sufficient for estimation until 27 July. After this date the rate of increase of total iron became even more rapid and an increasing proportion of it consisted of ferrous iron (Fig. 14). A large increase in ammonia content also occurred at this time. The water became clearer later in the summer, but the colour still continued to increase, indicating the accumulation of dissolved organic, possibly peaty, materials.

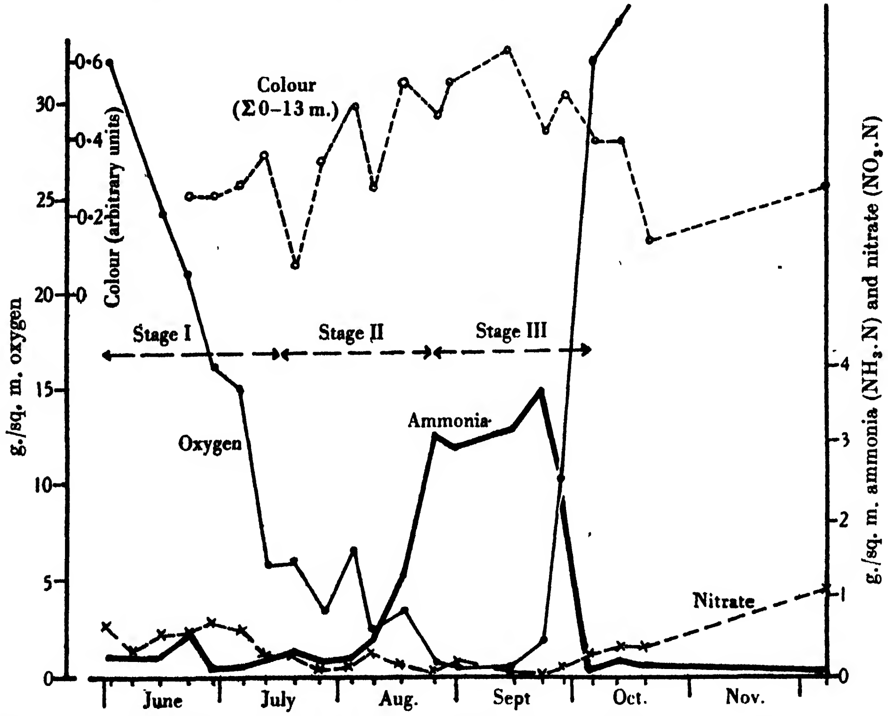


Fig. 13. Esthwaite Water, 1939. Variation in total content of oxygen, ammonia and nitrate in the hypolimnion water column above 1 sq. m. of mud surface. These totals were estimated by summation of concentrations at 10, 11, 12 and 13 m. Fig. 13 also includes total colour in the column 0–13 m.

The slowing up of the rate of increase of most substances (stage III) was observed during September. It cannot be readily estimated how far this was due to the gradual destruction of the hypolimnion by the progressive fall in level of the thermocline. A very rapid fall in total content of iron, phosphate and ammonia occurred at the completion of the overturn on 5 October, and during the period immediately preceding it. The fall was correlated with the rise in oxygen content in the hypolimnion, and may be considered as a rapid reversal of the changes produced by reduction in the spring. Corresponding decreases in alkalinity and conductivity are also apparent (Fig. 14). Total colour content of the water column fell off less rapidly, reaching a minimum value a fortnight after the completion of the overturn, and it was not until after this that the total nitrate content began to rise. It is not certain whether the fall in total silicate content at the overturn can be regarded as significant.

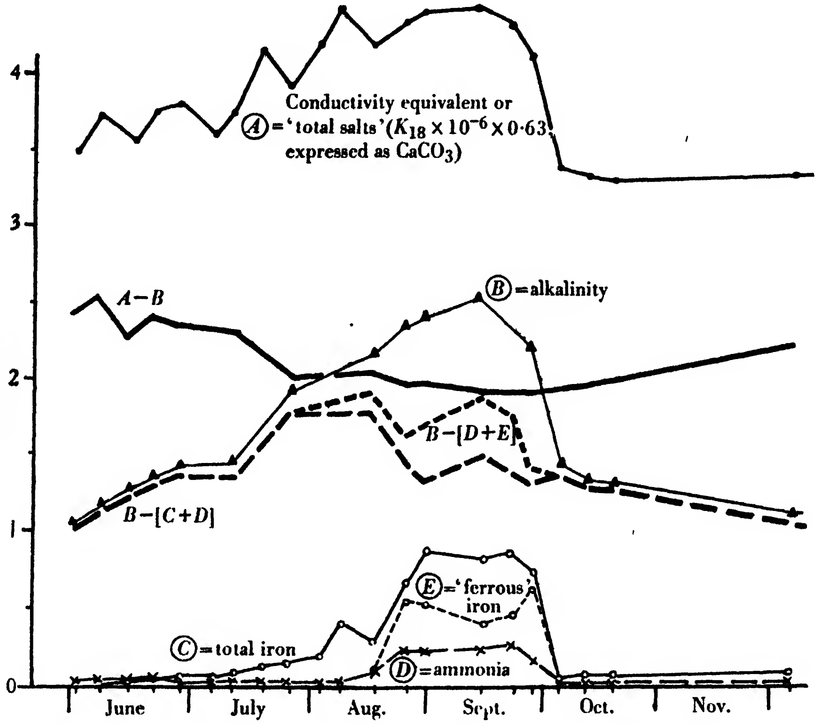


Fig. 14. Esthwaite Water, 1939. 'Total salt' and total 'excess base' (alkalinity) contents of the hypolimnion water column, compared with the respective contributions of iron and ammonia. Totals obtained by summation of 10, 11, 12 and 13 m. values and expressed in g.-equiv./sq. m. of mud surface. Iron other than 'ferrous' is assumed to be trivalent.

It is clear, however (Fig. 10), that the summer rise was due not only to production in the hypolimnion, but also to an increase in silica in the epilimnion from the minimal spring values. This rise occurred during both 1939 and 1940, and in spite of absorption by diatoms. Inflow water and littoral muds must be regarded as probable sources of this silica.

A consideration of the nitrogen relationships (Fig. 13) shows that ammonia production during stage II is much greater than the equivalent amount of nitrate reduced. A large part must therefore be produced by the mud. Under oxidizing conditions only traces of ammonia are found in the water and during thermal stratification no large increase occurred before August when the oxygen concentration had fallen to a low level and ferrous iron had appeared in the water. This suggests that nitrification (ammonia oxidation) occurs mainly at the mud surface, for if it occurred to any great extent in the water during winter circulation, i.e. if ammonia were given off from the mud and oxidized in the water, it would be expected that ammonia would have accumulated in the hypolimnion right from the commencement of thermal stratification, especially as nitrate reduction commenced at this time. The view that the oxidized mud surface is the main seat of nitrification is supported by the results of experiments, not described here, in which it was found that additions of ammonia to natural waters *in vitro* were not oxidized, but that considerable nitrate production occurred if small amounts of surface mud were added. If the period October to November may be taken as a fair comparison with August, it appears that the rate of supply of saline nitrogen to the water is much greater in the form of ammonia during stagnation (August) than as nitrate during circulation (October–November), and this takes no account of the fact that part of the winter increase must be attributed to an increase in nitrate content of inflow water (Mortimer, 1939). This suggests that, under oxidizing conditions at the mud surface, not all the ammonia diffusing into the mud surface is oxidized, but that a large part must be adsorbed.

Further information may be derived from an analysis of the increases in conductivity ('total salts') and alkalinity observed during thermal stratification and the corresponding decreases at the overturn (Fig. 14). In most natural waters only a portion of the cations (bases) is balanced by available mineral acid anions (${}^{-}\mathrm{Cl}$, ${}^{=}\mathrm{SO_4}$, ${}^{-}\mathrm{NO_3}$, ${}^{\equiv}\mathrm{PO_4}$, etc.). This portion with equivalent anions may be termed the 'neutral salt content', bearing in mind that in most waters dissolved salts are almost completely dissociated. Bases in excess of this portion may be considered to be combined with carbonate, or more commonly, bicarbonate. The amount of this 'excess base' is approximately that measured by the alkalinity determination. It is clear that part of the rise in alkalinity in the hypolimnion of Esthwaite Water must have been due to the increase in ferrous iron and ammonia (which may be considered to be in the form of bicarbonates) and possibly to the presence of ferric hydroxide as well. In order to determine how large this part is, the total content of alkalinity (expressed as $\mathrm{CaCO_3}$), total iron, ferrous iron and ammonia, in gram-equivalents per sq. m. for the water column 9·5–13·5 m., have been plotted against time in Fig. 14. Further, it was pointed out by Ruttner (1921) and Nümann (1936) that a part of the electrical conductivity of a water is due to substances producing alkalinity, the other part being attributed to the 'neutral salt content'. By determining the 'conductivity equivalent' of the alkalinity value (assuming it all to be due to calcium bicarbonate), these authors have enabled the relative magnitudes of the alkalinity and neutral salt fractions to be assessed from conductivity and alkalinity determinations. In all waters in which bicarbonate is the main anion (most fresh waters) a closely similar result may be achieved by multiplying the conductivity by Kitto's (1938) factor, 0·63, to convert it into 'total salt', and comparing this with alkalinity, both being expressed as $CaCO_3$. This has been done in Fig. 14 and, as only a relative comparison is required here, 'total salt (as $CaCO_3$)' has been plotted on the same scale of gram-equivalents per sq. m. as alkalinity, iron, etc.

Comparisons yield the following information. 'Total salt' minus alkalinity (line $A-B$) represents the equivalent content of the 'neutral salt fraction'. Bearing in mind the limitation of this comparison, no marked change in the 'neutral salt content' is apparent throughout the whole period under review. The slight decrease observed during the stagnation period may have been partly due to the fact that the alkalinity value may have included some substances, e.g. ferric hydroxide, in precipitated or unionized complex form, not included in the conductivity value, and partly due to sulphate reduction and precipitation as ferrous sulphide.

The line $B-(C+D)$ represents the alkalinity equivalent with the equivalents of total iron and ammonia subtracted. The marked rise shown by this line after 13 July must have been the result of the addition of bases other than iron and ammonia to the water column. The apparent fall after 17 August might be attributed to one or both of two causes. Either some part of the total iron, e.g. precipitated ferric iron, was not included in the alkalinity value, or bases other than iron and ammonia were removed from the water column. The possibility of adsorption on colloidal ferrous sulphide or humus colloids in water or mud should be borne in mind. No evidence is available to show to what degree the first cause may have been operative. If it is assumed that all the 'ferrous iron' (line E, Fig. 14) is included in the alkalinity value, but that ferric iron is not, then the content of 'excess base' other than ferrous iron and ammonia, line $B-(D+E)$, remained more or less constant until the middle of September, after which a decrease occurred at the overturn to a value which was almost identical with that on 13 July, before the summer increase began. This marked decrease at the overturn is clearly due to re-adsorption of bases, presumably mainly on the re-oxidized mud surface. The slow progressive fall in alkalinity during the early winter reflects a change which occurred throughout the whole of the water column and, as the conductivity remained constant during this period, this fall in alkalinity probably represents further adsorption of bases at the mud surface. As the difference between alkalinity and conductivity $(A-B)$ was even greater at the beginning of June, it may be supposed that this adsorption of bases proceeds throughout the winter.

The above considerations suggest that the sudden increase of bases other than iron and ammonia which occurred after 13 July represents the liberation of an adsorbed store of bases from the mud at a time when the adsorbing agents, possibly colloidal ferric complexes in the mud surface, were destroyed by reduction. It will be remembered that other evidence (acceleration of oxygen depletion and iron production) suggested that the mud surface had become completely reduced on this date.

The following description of events in the hypolimnion of Esthwaite Water may be advanced as a working hypothesis applicable to lakes in which deoxygenation occurs. In the early stage (I) of oxygen depletion, during which the oxygen concentration and the concentration gradient at the mud surface is relatively high, depletion proceeds at a relatively high rate. This rate decreases as the concentration gradient at the mud surface falls. Active nitrate reduction occurs during this stage. The next stage in reduction (II) is initiated when ferric iron is replaced by ferrous at the mud surface, which occurs at a fairly definite redox potential level (about $E_7 = 0{\cdot}25$ V.) and low oxygen concentration (about 0·5 mg./l.). The reduction of ferric iron results in the destruction of insoluble ferric complexes previously existing in the mud surface, and in the liberation to the water of bases, including ammonia, adsorbed on these complexes, as well as ferrous iron and other reducing material. The more rapid spread of these reducing substances by eddy diffusion in the water accelerates oxygen depletion. The depletion rate, of course, slows up finally as the available oxygen disappears. The removal of adsorbing complexes in the mud surface allows a more free exchange of ions to take place between mud and water. Rise in ionic concentration is mainly due to rise in alkalinity. The concentration of ions in the water increases rapidly at first (stage II), and then more slowly (stage III), until oxygen is re-introduced into the hypolimnion at the overturn. If the potential falls low enough before this occurs sulphate may become reduced and, if *p*H is sufficiently high. the sulphide may be precipitated as ferrous sulphide, which may cause a decrease in iron concentration.

A rapid reversal of these changes occurs at the overturn. Iron is precipitated from the water. Insoluble ferric complexes re-form in the mud surface, re-adsorbing much of the base content liberated during stagnation and reconstituting an adsorbent barrier in the surface mud layer to free exchange of ions between mud and water. Slow adsorption of bases from the water by this layer continues through the winter. At the same time nitrification of a portion of the ammonia supply from the lower mud proceeds at the mud surface.

Work designed to test this hypothesis both in Esthwaite Water and in artificial mud-water systems is described in succeeding sections. An attempt is made here to ascertain, as far as possible, whether these deductions may be confirmed by the examination of published data for other lakes. In one case only have sufficient physical and chemical data been published for a detailed comparison to be made. This comparison is especially valuable as the lake in question, Schleinsee (Einsele & Vetter, 1938), is in many ways similar to Esthwaite Water, a fact which is not so much a fortunate coincidence as might at first be supposed. The first author has already pointed out the importance of the iron cycle in lakes (Einsele, 1938) and has realized that oxidation-reduction processes and their influence on organic production are best displayed for study in lakes representing a transition between oligotrophic and eutrophic type and shallow enough to produce oxygen depletion in the hypolimnion.

The seasonal variation in total content of certain dissolved substances in the whole water column (0–11 m.) of Schleinsee, 1935, computed from values derived by inspection of Einsele & Vetter's figures, has been plotted (Fig. 15)

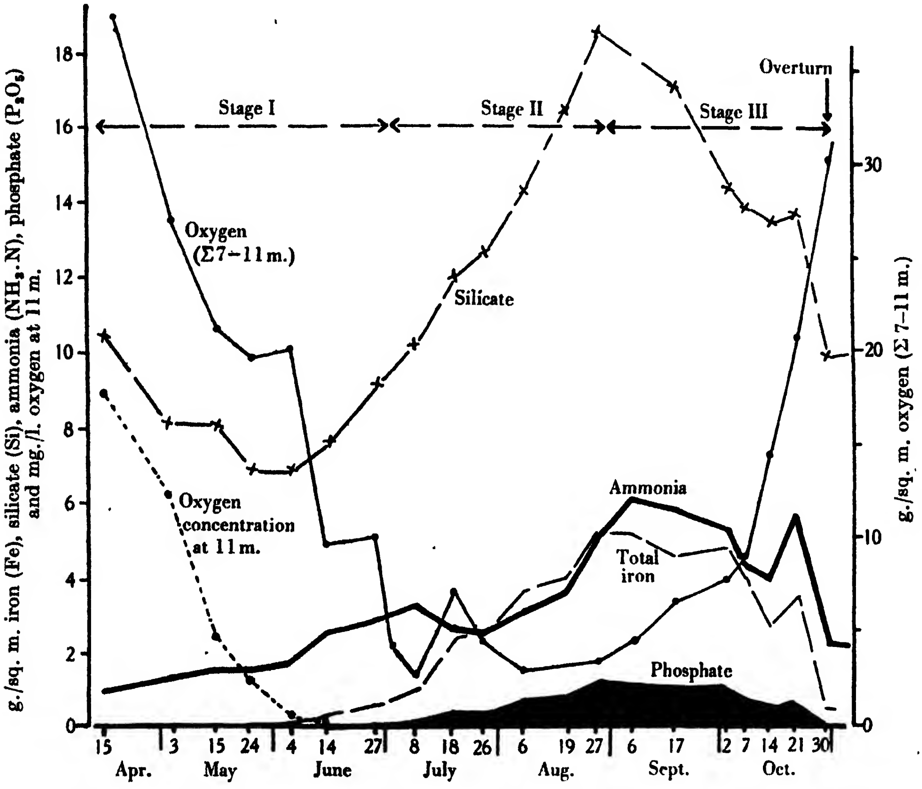


Fig. 15. Schleinsee, 1935. Total content of iron, silicate, phosphate and ammonia in the water column (0–11 m.) above 1 sq. m. of mud surface at the sampling station, compared with the oxygen content of the hypolimnion water column (7–11 m.) and the oxygen concentration in the lowest sample (11 m.).

is g./sq. m. on the same scale (with the exception of phosphate) as that employed for Esthwaite data (Figs. 12, 13). The depletion of oxygen in the hypolimnion (7–11 m.) followed a similar course to that found in Esthwaite Water. The depletion rate showed a marked decrease at the end of May. This was probably partly due to a decrease in concentration gradient at the mud surface, but the slightly negative depletion gradient which occurred between 24 May and 4 July must have been the result of some addition of oxygen to the hypolimnion by mixing from above or by photosynthesis. As in Esthwaite Water, a marked acceleration of oxygen depletion occurred after the oxygen concentration in the bottom sample (11 m.) had fallen below 0·5 mg./l., and this immediately preceded a rapid rise in iron and phosphate content and the appearance of ferrous iron in the water. The slow spring rise in ammonia content, which occurred in Schleinsee, was not observed in Esthwaite Water, but a marked increase during August, rising to a maximum in September, occurred in both lakes. Total ammonia production was about 50 % higher in Schleinsee. The contents of iron, phosphate, ammonia and also silica exhibited a marked fall at the overturn similar to that observed in Esthwaite Water. Decrease of silica during the spring was attributed by Einsele & Vetter to diatom growth in the epilimnion. The most important difference between Schleinsee and Esthwaite Water consists in the higher calcium content of the former. Alkalinity in Schleinsee is about ten times that in Esthwaite Water. It will also be noted that phosphate production in Schleinsee is also about ten times, while iron production is only about one quarter of, that in Esthwaite. These differences may be correlated with the higher calcium content of Schleinsee. (For convenience of plotting, phosphate is shown as P_2O_5 and on different scales in Figs. 12 and 15. Multiplication by 0·44 reduces these values to P.) Thus the Fe : P ratio in Schleinsee was about 8 : 1, while in Esthwaite Water, taking 1939 values not shown in Fig. 12, the ratio was about 200 : 1.

A striking increase of alkalinity in the hypolimnion and a simultaneous decrease in the epilimnion occurred during the period of thermal stratification. Einsele & Vetter consider these changes to result from biochemical precipitation of calcium carbonate in the epilimnion and re-solution in the presence of excess CO_2 in the hypolimnion. The total alkalinity in the whole water column (not figured here) showed little variation except for an unexplained sharp fall at the overturn. Thus a release of adsorbed bases to the hypolimnion as a result of the reduction of ferric adsorbing complexes cannot be demonstrated. The increase in alkalinity due to this cause in Esthwaite Water was approximately 0·5 g.-equiv./sq. m. (Fig. 14). It is possible that this amount is correlated with the total iron production or more closely with the amount of ferric adsorbing material present in the mud surface before reduction, so that the equivalent amount liberated in Schleinsee may be less than 0·5 g.-equiv./sq. m. In any case this amount makes up only about 3 % of the total alkalinity in that lake, and this may explain why an effect due to base liberation could not be detected.

From an extensive study of base-poor Japanese lakes, in which the masking effect of high alkalinity observed in Schleinsee is absent, Yoshimura (1932 *a*, *b*) has demonstrated that the increases in alkalinity, observed in the hypolimnia of those lakes in which de-oxygenation occurred, could be accounted for by increases in Fe, Mn, Ca and other bases. The increase in Ca was considered not to be due to the precipitation of $CaCO_3$ from higher levels, but to 'some other cause'. The description of events in Esthwaite Water suggests that this cause was liberation of adsorbed bases from the reduced mud surface.

Further evidence of similarity in the development of de-oxygenation in the hypolimnia of widely separated lakes is afforded by computations (results not given in detail) of the total oxygen depletion rate in those lakes, for which oxygen data have been published in sufficient detail, e.g. Wisconsin lakes; Mendota, Long Lake, Rainbow Lake (Birge & Juday, 1911), Schleinsee (Einsele & Vetter, 1938) and Waskesiu (Rawson, 1936). These computations, compared with those for Esthwaite Water 1939 and 1940, show that although considerable variations in the depletion rate occurred, there was in all cases a general tendency for the depletion rate to decrease as the oxygen concentration of the bottom sample (usually 1 m. from the mud) fell from about 5 to about 1 mg./l. This was probably due to the decrease of the oxygen gradient at the mud surface and was equivalent to stage I, already described for Esthwaite Water. This stage was followed in all cases by one of accelerated oxygen depletion (stage II). It has been suggested that this is the result of the liberation of reducing substances from the mud surface, after it has become reduced, and the increase in the rate of spread of these substances under the influence of eddy diffusion.

After completion of this manuscript, an important contribution to the study of stratified lakes has appeared (Hutchinson, 1941). Although a fuller discussion of this paper must be postponed, it is clear that Hutchinson's description of the development of stratification in Linsley Pond is in many ways similar to that given for Esthwaite Water.

(c) *Events under ice*

Conditions under ice provide opportunities for testing some of the deductions arrived at earlier. It was suggested that turbulence in the hypolimnion was induced chiefly by wind action. As this is absent under ice, it may be expected that the eddy diffusion coefficient A would be lower, that the spread of substances derived from the mud would be slower and that deoxygenation would be confined to a narrower zone than was the case during the corresponding period of summer stratification. An examination of Figs. 4–9 for Esthwaite Water 1939–40 shows how far these expectations were realized. During 7 weeks under ice, reduction at the mud surface had not proceeded as far, and the spread of iron and ammonia in the water was not as extensive as during the first 7 weeks after the commencement of summer thermal stratification at the end of May. The redox potential at the mud surface fell only to $E_7 = 0{\cdot}49$ V. and nitrate was not appreciably reduced. A comparison of Fig. 7 with other figures suggests that the rise in conductivity was greater, relatively to other dissolved substances, during the ice period than during June. There is some evidence however (Table 2) that not all this increase could be attributed to the mud. The only explanation that can be offered for the fact that the oxygen concentration was apparently lower and concentrations of other dissolved substances were apparently higher on 27 January than on 5 February, in all samples taken between 11 m. and the bottom, is that an error in depth determination occurred on the former date.

The conclusions in the preceding paragraph may be substantiated by the calculation of *A* using methods indicated previously. Estimates of *A* in both Esthwaite Water and Blelham Tarn 1940 (in which lake the findings in Esthwaite Water were confirmed) are summarized in Table 2. Results for Schleinsee from data obtained by inspection of Einsele & Vetter's figures (1938) have been included for comparison.

Table 2. *Estimates of the eddy diffusion coefficient* ($A \times 100$) *in lakes under cover of ice*

Lake	Esthwaite Water	Blelham Tarn	Schleinsee
Bottom (m.) at sampling station ...	14·0	13·2	11·6
Year	1940	1940	1935
Period	22. i.–22. ii.	6. i.–20. ii.	15. i.–15. ii.
Depth of estimation (m.)	13	12	11
	Mean values of $A \times 100$ for period under ice		
Data employed:			
Ammonia	0·5	0·8	1·8
Total iron	0·6	—	—
Conductivity	1·4	1·2	—
Phosphate	—	—	1·0
Alkalinity	—	1·0	—
Temperature	0·5	1·0	—

Ignoring the high value derived from conductivity data, which may have been the result of a conductivity increase from an unknown source in the water, the mean for Esthwaite Water may be taken as 5×10^{-3}. This is about one-sixth of that found at a similar level during summer stratification (Table 1), but is still over 200 times as great as the coefficient of molecular diffusion and about four times as great as molecular heat conduction in water. This indicates that convection currents prevent complete stagnation under ice. The distribution of temperature (Fig. 3) and the fact that the mud was consistently at a higher temperature than the water just over it, suggest that the heat given off to the water by the mud may be responsible for such slow convection currents. This heat represents that stored by the mud since the summer, and possibly also some heat produced by organic decomposition. A more rapid loss of heat from the mud during the autumn is prevented by extremely slow conduction in the mud (cf. Birge *et al.* 1928). Other supplies of heat may be neglected. It is hoped to discuss this subject in more detail in a later communication (Mortimer, in prep. I).

It will be noted that *A* in Blelham Tarn is appreciably higher than in Esthwaite Water. Also in Schleinsee *A* under ice is not significantly less than that in the hypolimnion during August (cf. Table 1). No explanation can be offered at present for this difference, but in Blelham Tarn it was noted that numerous large marsh gas bubbles collected under the ice, especially in the neighbourhood of the inflow streams, but also in the middle region at the sampling station. It is probable that turbulence associated with the rise of these bubbles to the surface was sufficient to increase A significantly (cf. Rossolimo & Kusnetzowa, 1934). The organic content of Blelham Tarn mud is appreciably higher than that of Esthwaite Water (Misra, 1938), but it seems doubtful whether this difference produces a sufficient increase in heat of decomposition to affect convection currents above the mud significantly.

The rise in concentration of certain solutes observed in the water just under the ice is of interest (see Figs. 4, 7). To determine whether these had been eliminated from the ice during the freezing process, blocks of ice were cut out with a narrow-bladed saw, commencing the cut in a hole bored with a brace and bit. The blocks were washed with distilled water and melted in clean Pyrex vessels. For 'dissolved' oxygen determinations, blocks were washed, dried and melted under medicinal paraffin. To obtain an undisturbed sample of water from just under the ice some distance from the hole, a rubber tube about 2 m. long, one end of which was mounted in a cork, was inserted through a small hole in the ice. The cork was designed to float the end of the tube up against the lower surface of the ice some distance from the hole. The sample was then sucked through sampling bottles by means of a bicycle pump with reversed valve, as described in the next section. The results are summarized in Table 3.

Table 3. *Dissolved content of* (*a*) *ice*, (*b*) *water just below ice and* (*c*) *water at* 5 *m. depth in Esthwaite Water*, 12 *January* 1940

Results of chemical analysis expressed in mg./l. of water.

	(*a*) Ice (molten)		Water	
	Upper clear layer	Lower cloudy layer, containing bubbles	(*b*) Immediately under ice	(*c*) At 5 m. depth
Temperature, ° C.	Assumed to be 0		1·4	3·9
Dissolved oxygen, mg./l.	5·3	10·0	14·3	11·5
Dissolved oxygen, % saturation	35	68	103	88
Conductivity ($K_{18} \times 10^{-6}$)	4	3	75	65
Alkalinity ($CaCO_3$)	0·5	0·7	15·6	13·6
Colour (arbitrary units)	None	None	0·01	0·01
Ammonia (NH_3)	None	None	0·10	0·06
Nitrate (NO_3)	None	None	1·4	1·2
Sulphate (SO_4)	None	None	9·3	8·8
Iron (total Fe)	None	None	0·24	Trace
*p*H	6·0	—	6·9	6·8

The removal of dissolved salts from ice on freezing was therefore practically complete. These salts accumulated in the water just under the ice. From its chemical composition the water obtained from Esthwaite ice would be classed as good quality distilled water. It is probable that the oxygen found in the ice was not in true solution but entrapped in the form of bubbles, which were seen to have accumulated in the lower cloudy layer. The *p*H (6·0) in water derived from ice melted under paraffin suggests that some CO_2 was also retained.

II. CHANGES IN REDOX POTENTIAL AND IN CONCENTRATIONS OF DISSOLVED SUBSTANCES IN ARTIFICIAL MUD-WATER SYSTEMS, SUBJECTED TO VARYING DEGREES OF AERATION

It was suggested in the preceding section that changes in redox conditions occurring at or near the mud surface during de-oxygenation of the hypolimnion in lakes are associated with and probably control marked changes in the rate of exchange of ions between mud and water. The following experiment was designed to study these changes more closely in 'artificial lake systems' under laboratory control.

METHODS AND EXPERIMENTAL PROCEDURE

Several Petersen grab samples of typical Windermere mud were taken from about 30 m. depth off Wray Castle Boat House. The surface brown layer containing ferric iron was scraped off and kept separately from the lower reduced dark grey mud, which was stirred to obtain a uniform sample and then poured into three glass tanks (rectangular battery jars, 15 × 20 cm., 25 cm. deep) to a depth of about 3 cm. The tanks were then slowly filled with tap water without disturbing the mud. The surface scrapings were also stirred, mixed with a little tap water and divided into three approximately equal portions, one of which was added to the water of each tank in such a way that an even layer was deposited on the mud surface. In this way an attempt was made to imitate a natural mud. The water in the tanks was siphoned off and the mud allowed to stand exposed to the air for several days. After this, but not before, it was found possible to run lake water into the tanks very slowly to a depth of 20 cm. (6 l. in all) so that it remained clear. The tanks were kept in the laboratory, exposed to light, but shielded from dust. The temperature of the water in the tanks rose gradually, with slight variations, from 14 to 20° C. during the course of the experiment. After standing for a week to attain approximately stable conditions, the surface brown 'oxidized layer', viewed through the glass sides, was about 7 mm. deep in all tanks. The mud surface showed a tendency to crumble and become detached in small cakes when measuring instruments were inserted and removed, and was not as flocculent as the natural mud surface in the lake.

At this stage a series of determinations were carried out on all three tanks. The results (zero on the time scale, Figs. 18–20) showed that conditions in each tank were sufficiently comparable for the purposes of the experiment. Each tank was then subjected to a different treatment, described below, and the following determinations repeated on all three tanks at intervals.

Electrical conductivity. With the instrument and electrodes previously described, measurements were made at various points in each tank, in the water and at three depths in the mud (0·5, 1·5 and 2·5 cm.). It was found that horizontal variation was negligible in the water and small in the mud. Values given in Fig. 18 are mean values for each level. The electrodes, which were of robust pattern, are shown in Fig. 16 C.

Redox potential. Following the potentiometric technique employed by Pearsall & Mortimer (1939), using a saturated KCl-calomel half-cell and saturated KCl agar bridges, redox potential was measured at small depth intervals above and below the mud surface with a series of bright platinum electrodes, the arrangement of which is shown diagrammatically in Fig. 16, and in Fig. 24, § III. Each electrode consisted of a strip of platinum foil 10 × 2 mm., welded on to a frame of stout platinum wire of the same dimensions for support. An efficient weld was achieved by hammering the red hot pieces of metal together on a carbon block. The electrode was mounted as shown in Fig. 16B by fusing the wire into the end of a narrow glass tube (75 cm. long for use with the surface mud sampler described in the following section), and internal connection was made with a drop of mercury and copper wire in the normal way. Twelve such electrodes were arranged around cork centres in such a manner that the metal blades radiating from the centre came to lie at fixed depth intervals on a descending spiral, as shown in Fig. 16A and Fig. 24, § III. Thus, when this 'compound electrode' was lowered vertically into the mud, the electrode at each level cut edge-on into mud,

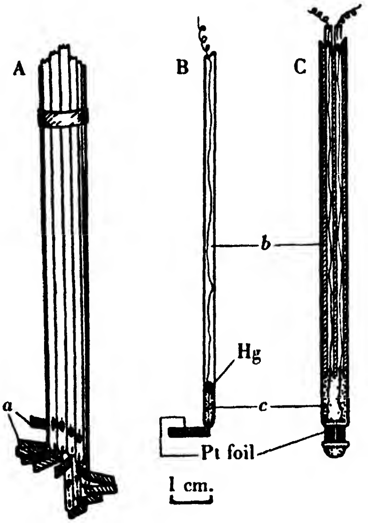


Fig. 16. Electrodes for the measurement of redox potential and electrical conductivity. *a* = frame of s.w.g. Pt. wire; *b* = copper lead enclosed in glass tube; *c* = glass seal around 42 s.w.g. Pt. wire.

which was undisturbed by the passage of lower electrodes. Each electrode may be considered to register the mean potential of a panel 2 mm. deep at the depth to which it is lowered. The depths usually chosen for measurement were 50, 10 and 1 mm. above and 1, 2, 3, 5, 7, 10, 13, 16, 19 mm. below the mud surface. For measurements described in the next section on lake muds *in situ* in the sampling tube of the surface mud sampler, four similar electrodes, which could be readily adjusted at different levels, were added to the system for measurements at greater depths below the mud surface. These were arranged to slide up and down in holes in the cork centres. The arrangement of the electrodes for these measurements is shown in Fig. 24, § III. The copper lead from each electrode was fixed in order of electrode depth on a celluloid strip, and could be selected for connection with the potentiometer terminal by means of a clip lead.

Both in natural muds (see next section) and in muds in the tanks the electrode potentials fell rapidly during the first hour after insertion. Usually a fairly steady state was reached after 1–2 hr. A slow negative drift was observed over a period of days. Potential values given in this and the next section refer to measurements made 2 hr. after insertion. E_h and, where possible, *p*H were recorded and all potentials were reduced to a comparative basis of E_7, i.e. E_h at *p*H 7·00, assuming a rise in one *p*H unit to be equivalent to a decrease of 58 mV. (cf. Pearsall & Mortimer, 1939). E_7, expressed in volts, was chosen in preference to E_5 (cf. Pearsall & Mortimer, 1939) as 7·00 was nearer the actual *p*H of the media investigated. After every few determinations the electrodes were tested by immersing them in a well mixed sample of reducing mud of sufficient volume to cover them all. Usually readings on all electrodes agreed to within ± 10 mV. Occasional anomalous behaviour of single electrodes will be discussed in a future communication (Mortimer, in prep. V), in which the measurement and interpretation of redox potentials and *p*H in lake muds will be dealt with more fully. If agreement of the above order was not obtained the electrodes were cleaned with dichromate-sulphuric acid and rinsed well. Between determinations the electrodes were kept immersed in distilled water.

*p*H *determination.* It is probable that the most satisfactory method of measuring *p*H at small depth intervals above and below the mud surface would be with a glass electrode of suitable 'micro' pattern. In the absence of the necessary equipment, a modification of the quinhydrone method used for soils was employed. A critical study of the application of this method to muds showed that, owing to the reducing and unbuffered characters of most of the muds investigated, it was necessary to maintain the mud/quinhydrone ratio within narrow limits to obtain reproducible results. Even so, the following technique produced results which were normally only reproducible on the same mud sample to within 0·1 *p*H unit. To approximately 5 c.c. of mud roughly an equal volume of distilled water and from 30 to 50 mg. quinhydrone was added in a glass dipper. The mixture was shaken and the potential measured in the usual manner after 2–5 min. Difficulty in the measurement of *p*H in lake muds by the quinhydrone method was also experienced by Karsinkin & Kusnetzow (1931). However no advantage was discovered, in the present work, in employing the technique suggested by them, namely the measurement of the potential in the supernatant liquid after the quinhydrone-mud mixture has been allowed to settle.

Extremely high apparent *p*H values (between 8 and 9) were found with the quinhydrone electrode at the oxidized surface of some muds. These were almost certainly anomalous and probably due to the presence of manganic compounds. Such compounds in soils (Wright, 1939) are reduced by quinhydrone to manganous hydroxide which raises the *p*H. In these cases the *p*H of the mud was either assumed to be the same as that of the water just over it, or colorimetric determinations were made with indicators in 0·5 % agar. This method will be described later (Mortimer, in prep. V).

In the work on cores of natural muds described in the next section, *p*H was determined on samples obtained by slicing the core up into layers, usually approximately at centimetre depth intervals. The sample from each layer was well mixed and its *p*H value was taken to be the mean value for the depth panel concerned. From this data, the probable *p*H at the depths at which E_h measurements had been made was determined by graphical interpolation. The probable E_7 value was then computed and the result expressed to two figures. A consideration of the reproducibility of E_h and *p*H values shows that in many cases it is doubtful if the second figure is significant. Even so the results are sufficiently accurate for the purposes of this paper, as the range of E_h values encountered was large. *p*H in the water was determined colorimetrically. During the experiment described in this section it was not possible to remove samples of the mud for *p*H determination. Determinations made with the quinhydrone electrode at the end of the experiment showed that the mean value of the surface and lower mud in the aerated tanks was 6·3 and 6·4 respectively, while in the anaerobic tank the equivalent values were 6·6 and 6·7. These *p*H values were employed to calculate a probable E_7 value at different depths in the mud throughout the course of the experiment.

Chemical analysis was carried out on samples of water removed from the tanks immediately after determinations of redox potential and conductivity had been made. The sampling arrangement employed consisted of a glass tube supported with one end an inch or so above the mud surface. This lower end was turned up to avoid disturbance of the mud during the sampling operation. The tube was connected by rubber tubing through a tap to (1) a 125 c.c. bottle of the type used for oxygen determination, (2) a 50 c.c. flask for CO_2 determination (described below) and (3) a bottle of 400 c.c. capacity, in that order in such a manner that, when the system was partially evacuated by means of a bicycle pump with reversed washer, water was sucked first through the oxygen bottle and then through the CO_2 flask, expelling the air in both of these in the process. The tap was kept closed until a slight vacuum had been created in the system by a few strokes of the pump. Otherwise there was danger of disturbing the mud surface. Water was sucked through until 400 c.c. had arrived in the last bottle. The tap was then closed and the apparatus disconnected. In this way an adequate flushing of the oxygen bottle and CO_2 flask was ensured. Samples for oxygen determination were treated in the usual way, those from the anaerobic tank being pre-oxidized with bromine, according to Alsterberg's modified procedure (Ohle, 1936*b*). During the latter stages of the experiment, concentration of solutes in the anaerobic tank rose sufficiently to enable all determinations to be carried out on smaller samples.

The estimations made on the sample in the larger bottle are listed in Figs. 19 and 20. The methods employed were either standard methods or those described in the preceding section, with the exception of 'oxygen absorbed from permanganate' which was determined on a 50 c.c. sample, to which 5 c.c. $N/80$ $KMnO_4$ and 5 c.c. 25 % H_2SO_4 had been added, and which was incubated at 40° C. for 4 hr.

Dissolved carbon dioxide was determined by a modification of standard procedure. Although simple in principle, standard procedure (titration with standard alkali or carbonate using phenolphthalein) involves the difficulty of adequate stirring without introduction of atmospheric CO_2. In the method adopted here the sampling vessel was also the titration vessel. The standard alkali was weighted with Glauber's salt and the phenolphthalein weighted with glycerine according to the instructions of Maucha (1932). The sampling and titration flask was prepared as follows: Pure molten paraffin wax (*p* in Fig. 17 A) was allowed to solidify in the bottom of a 100 c.c. volumetric flask and strips of glass, designed to function as baffles (*g*), were embedded in the wax in the manner indicated. After the sample had been obtained in the manner described above, a portion was removed by pipette for *p*H determination, leaving 50 c.c. in the flask to which 10 drops of phenolphthalein was added. Titration was carried out with the arrangement shown in Fig. 17 A, with the tip of the burette extension under the surface of the liquid. The bulb (*b*) on this extension ensured that all the alkali was delivered below the surface of the sample and that none collected on the side of the neck. Due to its greater density the alkali sank to the bottom of the flask. Rotation of the flask with the neck held between the hands ensured a rapid thorough mixing of the heavier reagents and the sample without undue agitation of the small surface exposed to the air in the neck of the flask. It was not considered necessary to cover this surface with medicinal paraffin, although this could be done in cases in which it is required to carry out a titration by similar methods in the complete absence of air.

Further treatment of the tanks. After the preliminary series of determinations had shown that conditions were practically identical in all three tanks, each was subjected to different treatment. One, the 'artificially aerated tank', was subjected to continual aeration by means of the apparatus shown in Fig. 17 B. The wide tube (*a*) was adjusted at such a height that, when suction from a filter pump was applied at *b*, water was sucked up from the tank through the tube *c* of 4 mm. bore. This continued until the level of water in the tank had fallen sufficiently to admit air through *c*. In this way the partial vacuum inside *a* was destroyed and the water began to flow back to the bottom of the tank through tube *d* of 2 mm. bore. The water level in the tank of course rose at the same time, but an interval elapsed before stable conditions were re-established at the lower end of *c*, so that in practice air continued to bubble through the water in *a* and no water was sucked up until *a* was practically empty. The rate of this continuous aeration and circulation could be varied by varying the suction of the filter pump.

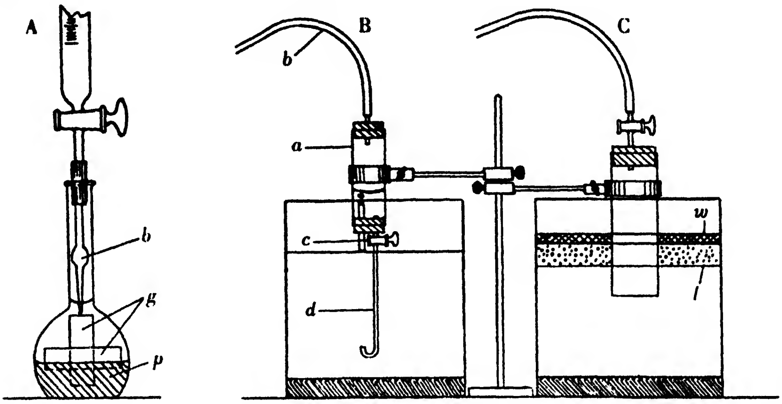


Fig. 17. Titration flask for carbon dioxide determination. Arrangement of 'artificially aerated' and 'anaerobic' tanks. *w* = paraffin wax; *l* = liquid paraffin.

A second tank ('aerated tank') was allowed to stand with the water surface exposed to the air. All three tanks were shielded from dust. The water surface in the third tank ('anaerobic tank') was covered with medicinal paraffin to a depth of about 2 cm., after a wide glass tube had been fitted as shown in Fig. 17 C to act as a shaft for the insertion of measuring instruments and sampling tube into the tank without bringing them into contact with the liquid paraffin. After measurements, the water level in the shaft was raised by suction until all the air was withdrawn; the tap was then closed. Just before each series of measurements, air was admitted to the shaft and the water level was allowed to fall gradually in order not to disturb the mud surface. The rubber bung was then removed and electrodes inserted. Naturally some air was introduced during measurement, but this did not disturb the course of the experiment. More serious trouble was encountered when it was discovered that the liquid paraffin layer was not an effective barrier to the diffusion of atmospheric oxygen. It was found necessary to employ an additional seal of paraffin wax. This was conveniently done by running molten wax down a wide gently inclined plane of cardboard on to the surface of the liquid paraffin. More violent pouring caused the wax to plunge down into the water and solidify there in lumps. This surface solid crust of wax, which formed an effective barrier to the diffusion of gases, could sometimes be made to follow changes in level occurring during sampling and measurement, but cracks often developed and the wax had to be removed and the crust recast.

RESULTS

Results are presented in Figs. 18–20, in which concentrations of dissolved substances in the water are plotted against time. Redox potential and conductivity data are incorporated in depth-time diagrams on the same time scale. The concentrations recorded in the figures are expressed as mg./l. in the actual sample. They have not been corrected for changes in relative volume of water and mud resulting from the removal of samples. It is clear that a part of the increase in some dissolved substances in the anaerobic tank, from which more samples were taken, was due to the decrease in water volume. As the purpose of the experiment was to detect large qualitative differences between aerated and anaerobic tanks, no correction has been made for this. If the results had been corrected for volume, it is by no means certain that the corrected values would bear any relation to natural rates of production, as it is not known whether the concentration of any one ion in the water represents a uniform concentration throughout the whole mud + water volume, or an equilibrium between mud and water, which is maintained irrespective of volume changes in the water. For estimations of the natural ionic production rates of lake muds, similar experiments with larger tanks and with a deeper layer of mud are necessary, in order that the volume of water removed in the sample may be small in comparison to the total volume, and that the production of ions by the mud shall not be limited by shallow mud depth.

Data from the 'artificially aerated tank' have been omitted here, as they were very similar to those obtained in the tank which was aerated by exposure to the air. The only marked difference was that the changes occurring in both tanks took place more rapidly in the artificially aerated one. It therefore appears that convection currents were sufficient to maintain fully aerated conditions in the standing tank ('aerated tank' in Figs. 18–20).

Redox conditions in (a) the aerated tank. Isovolts are drawn in Fig. 18 for intervals of 0·06 V. The depth of the isovolt ($E_7 = 0{\cdot}24$ V.)—thick line in the figure—approximately corresponded with the lower limit of the surface chocolate-brown 'oxidized layer', containing ferric hydroxide, as viewed through the side of the tank. This is in agreement with the finding of Pearsall & Mortimer (1939) that ferrous iron replaced ferric if the redox potential fell below this level. The depth of the isovolt $E_7 = 0{\cdot}24$ V. below the mud surface may therefore be considered to register the thickness of the oxidized surface

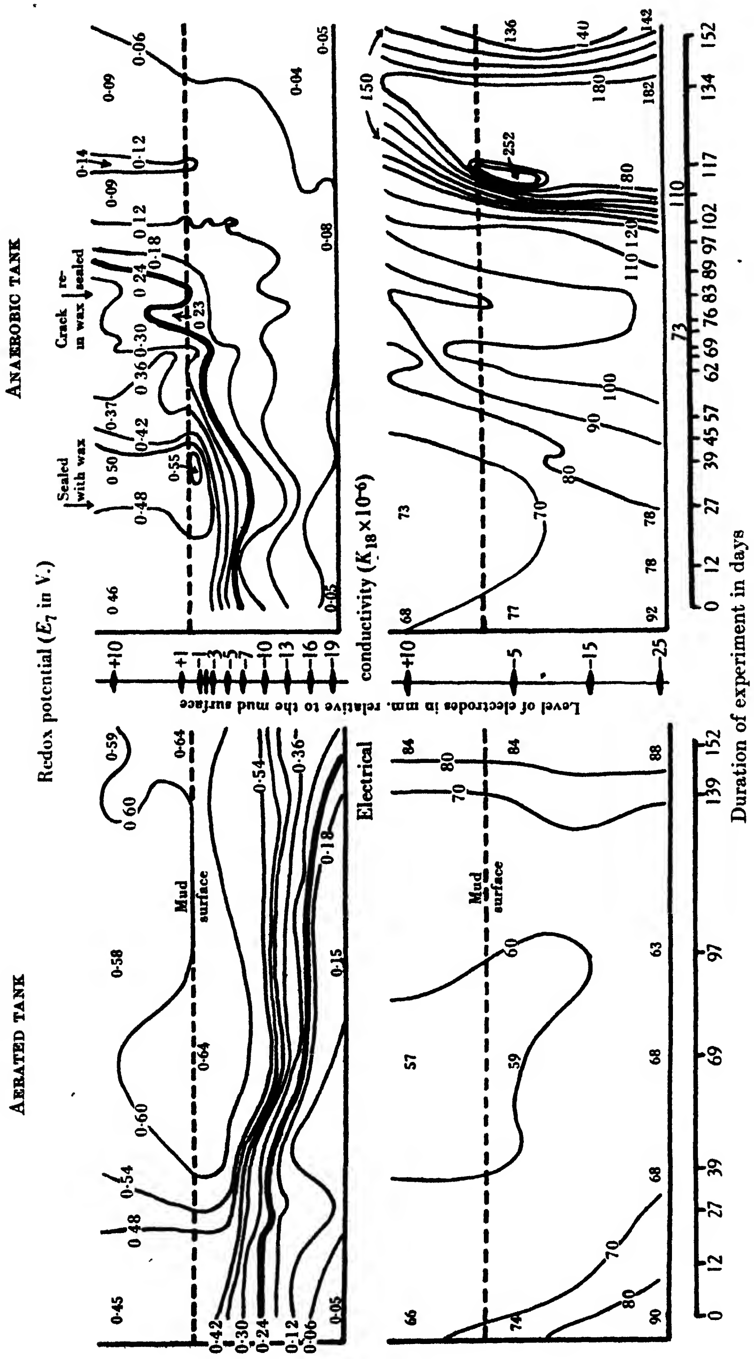


Fig. 18. Depth-time diagrams of the distribution of redox potential and electrical conductivity in the 'aerated' and 'anaerobic' tanks.

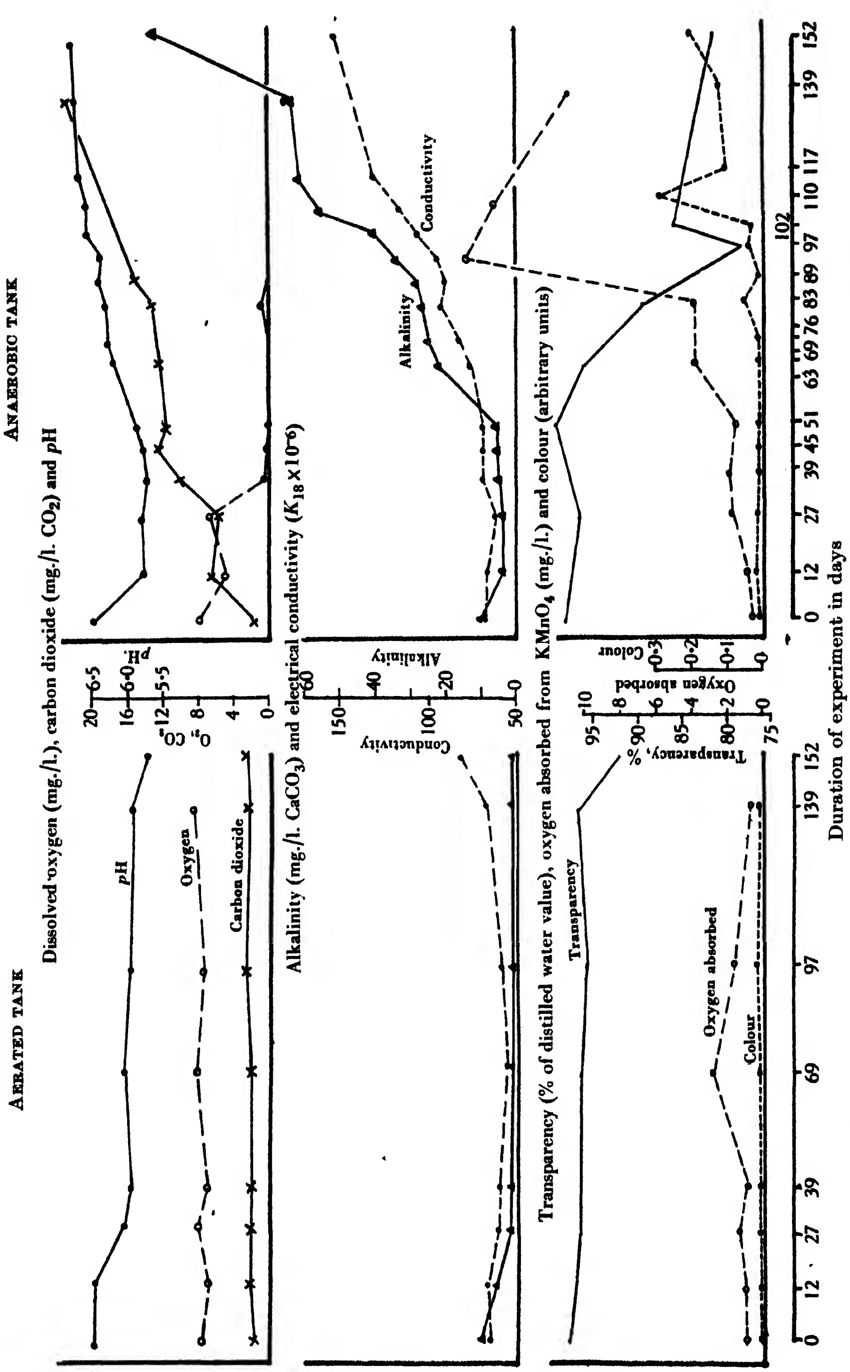


Fig. 19. A comparison of variations in some physical variables and concentrations of dissolved substances in the aerated and anaerobic tanks.

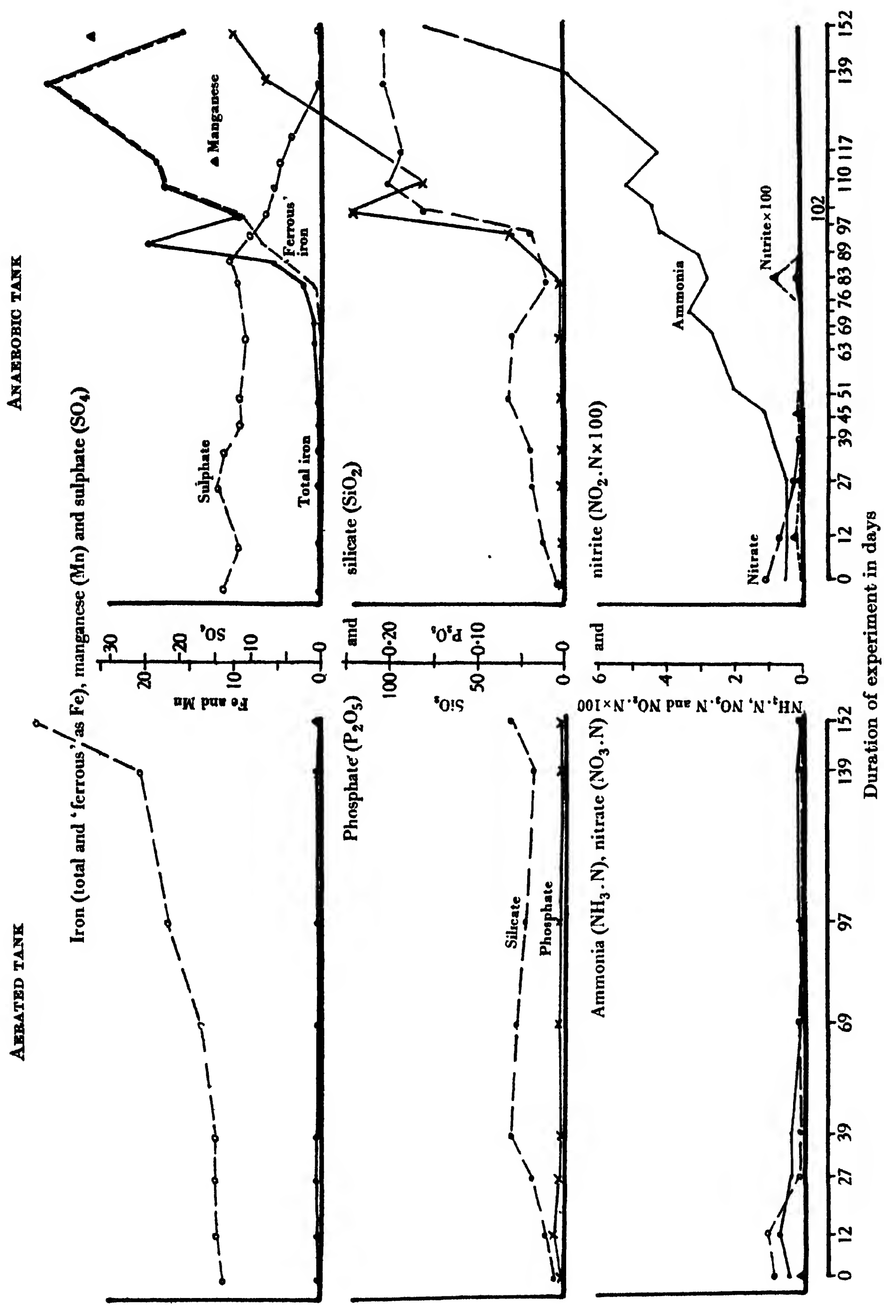


Fig. 20. A comparison of variations in concentration of some dissolved substances in the aerated and anaerobic tanks.

layer. In the aerated tanks this gradually increased during the course of the experiment.

(*b*) *The anaerobic tank.* From the time when the tank was effectively sealed from the atmosphere by paraffin wax (27 days), the isovolt $E_7 = 0{\cdot}24$ V. began to rise to the mud surface, reaching it at 70 days, at which time the mud surface had considerably darkened in colour and the dissolved oxygen in the water had disappeared. Previously to this, nitrate had become completely reduced in the water (51 days) and the ammonia concentration had begun to rise (Fig. 20); at this time the potential in the water was approximately $E_7 = 0{\cdot}36$ V. The difference between the marked vertical stratification of redox potential in the mud and the lack of such stratification in the water is striking. The potential values at 50 mm. above the mud surface have been omitted from the figure as they were almost invariably the same as those found at +10 mm. This difference may be considered to be due to the fact that much of the reducing material is in immobile form in the mud and that transport of dissolved substances within the mud by molecular diffusion is slow in comparison with convection currents and associated eddy diffusion in the water.

Changes in the water of the anaerobic tank. The most striking result obtained during the experiment was the rapid rise in concentration of iron, ammonia, silicate, phosphate, alkalinity, conductivity and substances reducing permanganate observed in the water of the anaerobic tank, after the potential at the mud surface had fallen below $E_7 = 0{\cdot}24$ V., i.e. after the oxidized surface layer had disappeared. This rise in concentration was maintained, although for most substances at a slower rate, during the subsequent course of the experiment. As stated earlier, a part of the considerable rise in concentration observed in some cases toward the end of the experiment must be attributed to a considerable decrease in water volume resulting from the removal of samples.

A more detailed examination of events after the destruction of the surface oxidized layer shows other points of interest. These events also exhibit a marked parallelism with those found to occur during reduction in the hypolimnion in Esthwaite Water during 1939. The rise in ammonia-nitrogen far exceeded the equivalent amount produced by nitrate reduction, and must therefore have originated from the mud. Nitrite appeared in small quantities during the period of nitrate reduction, but had disappeared by the time the potential in the water had fallen below 0·30 V. The rate of increase of iron, silicate and phosphate, as well as of substances reducing permanganate was greatest while the potential in the water fell from 0·18 to 0·12 V. Iron, phosphate and manganese continued to increase in concentration after this, whereas silicate showed no further rise and substances reducing permanganate showed a decrease. All the iron was in ferrous form after the potential had fallen below 0·12 V.

During the initial stages of the experiment, the rate of increase of CO_2 in the anaerobic tank was approximately proportional to the decrease in oxygen concentration. This result might be expected if it is assumed that most of the oxygen was absorbed in the oxidation of organic material and in such reactions as the production of ferric hydroxide from ferrous bicarbonate. The slow rise in CO_2 concentration after the disappearance of the oxygen cannot be taken as evidence of anaerobic CO_2 production, as it is probable that this increase is due to the accumulation of CO_2 produced as a result of the introduction of a little oxygen at each series of measurements.

A crack which developed in the wax seal just before 83 days had an interesting effect on conditions in the water. The isovolt $E_7 = 0{\cdot}24$ V. was pushed down to the mud surface, a small amount of oxygen was detected in the water, and traces of nitrite and nitrate were found. The introduction of oxygen also resulted in the oxidation of a large amount of iron, which was found in suspension in ferric form, resulting in a decrease in transparency of the water. A decrease in silicate concentration also occurred at the same time.

The sulphate concentration began to fall slowly after the tank had been effectively sealed from the atmosphere. This fall may have been due to the diffusion of sulphate into the mud and its reduction there in regions of lower potential. After the potential in the water had fallen below 0·10 V., reduction of sulphate proceeded more rapidly. It had disappeared when the potential in the water had fallen to 0·06 V. The sharp fall in iron (mainly ferrous) concentration, which occurred at the same time may be considered to have resulted from the precipitation of ferrous sulphide. This was associated with a fall in conductivity and transparency, and with a sharp rise in ammonia and alkalinity. During this period the mud surface became black, presumably as a result of accumulation of ferrous sulphide.

Electrical conductivity of the mud in the anaerobic tank rose steadily during the period of reduction of the mud surface, later rising rapidly to over 200 at the mud surface. This rise may have been partly due to the liberation of adsorbed ions as adsorbing complexes were destroyed by reduction. The sharp fall in conductivity which occurred after the maximum at 117 days may have been the result of the precipitation of ferrous and sulphide ions as ferrous sulphide. It is also possible that some adsorption of ions on colloidal ferrous sulphide took place.

Conditions in the aerated tank. None of the changes described above were observed in the aerated tank, in which the oxygen concentration in the water remained high and the isovolt $E_7 = 0{\cdot}24$ remained well below the mud surface. Apart from a slight initial fall in conductivity, a more rapid initial fall in pH, alkalinity, nitrate and ammonia and a subsequent slow rise in sulphate and conductivity, little change occurred in the concentrations of dissolved substances in the water.

Discussion

Changes in the 'aerated tank' may be interpreted as follows: The initial fall in alkalinity was considerably more rapid than the corresponding fall in conductivity. This indicates adsorption of bases, of which ammonia formed a large proportion. This resulted in a fall in *p*H, as the CO_2 concentration remained fairly constant. The strongly adsorbent properties of lacustrine muds, especially in the surface layers, have long been recognized in commercial fish-pond practice. Inorganic fertilizers added to ponds are strongly adsorbed on the mud and released to the water at a slow rate. For instance, the beneficial effect on the fish crop of liming or phosphate manuring in one year can be detected in subsequent years (Demoll, 1925). From the experiment described here and also from observations during the winter of 1939 in Esthwaite Water, there is reason to suppose that this adsorbing influence is exercised by the oxidized mud surface. It is clear that continuous adsorption must have occurred in the mud surface of the aerated tank, for there is no reason to suppose that organic decomposition in the mud had stopped, and there is no other explanation of the lack of rise of conductivity in the whole system, including the mud.

The decrease in nitrate in the aerated tank may, at first sight, appear surprising, as it has been shown in experiments mentioned in the preceding section that nitrification occurs at the oxidized mud surface. A similar observation of the disappearance of nitrate above pond muds with oxidized surface was made by Lind (1940). Some of the nitrate produced at the mud surface must diffuse down into the lower mud and become reduced there. It may be suggested that both in this and in Lind's experiment, in which the water volume was comparatively small, the rate of nitrification was not sufficient to make good the loss of nitrate from diffusion into and reduction in the mud.

The results obtained in the anaerobic tank show that, when the connection between the mud surface and the atmosphere through the water as intermediary is interrupted, the adsorbing influence of the mud surface (observed in the aerated tank) is removed. As events, which may be described as the rapid release of adsorbed materials, occurred at the time when the isovolt $E_7 = 0{\cdot}24$ V. had reached the mud surface and when all the ferric iron in the mud had become reduced, it may be suggested that the adsorbent properties of the oxidized mud surface are largely due to the presence of colloidal ferric complexes. The removal of these complexes on reduction of the mud surface, may be considered to result, not only in the liberation of adsorbed ions, but also in a much less impeded exchange of ions between mud and water, as shown by the continued rise in most dissolved constituents following the initial rapid rise just after the mud surface had become reduced. This continuous production during the latter part of the experiment was of course slower, expressed per unit area of mud, than that indicated in Figs. 19 and 20. If corrections had been made for change in water volume, this would demonstrate more clearly the contrast between the initial rapid rise and the following slow increase in concentration.

While a more detailed description of the adsorbing agents in the mud surface must be left to future work, some speculation as to their nature is permissible. Mattson (1935) has suggested that the adsorbent complex which is transported and precipitated in peaty podsols is a ferri-silico-humate. It is possible that a similar complex exists in the oxidized mud surface. If this is so, the rise in silica concentration during the period of reduction of the mud surface might be considered to result from the destruction of this complex. The fall in silica concentration associated with considerable precipitation of ferric iron after the introduction of oxygen through a crack in the wax at 83 days, may have resulted from the re-formation of this complex, and the subsequent rapid rise in silica may have been produced when the complex was again reduced. No marked increase of silica occurred after 110 days. The source of silica, whatever it may have been, appears to have become exhausted. Mention should also be made of the existence of ferric hydroxide and ferric phosphate in the oxidized mud surface (cf. Einsele, 1938). Ferric hydroxide is probably largely in colloidal form and may exert a considerable adsorbing influence. The sharp rise in phosphate concentration at the same time as disappearance of ferric iron in the water (97–102 days) is in agreement with Einsele's (1938) observation that large amounts of phosphate are bound as insoluble ferric phosphate in the surface of oxidized muds, and liberated in soluble form on reduction. The possibility that an organic constituent, possibly of the humus type, forms a part of the adsorbing complex in oxidized muds, is suggested by the rise in colour and in the concentration of substances reducing permanganate which occurred in the water after the mud surface had been reduced. The increase in permanganate reduction was considerably greater than the equivalent reduction due to ferrous iron content alone.

The similarity of events in the water of the anaerobic tank and in the hypolimnion of Esthwaite Water has been pointed out before. There are, however, important differences. In Fig. 21 a comparison is made between the increase in conductivity ('total salts'), alkalinity and other bases (ammonia, iron and manganese). The assumptions involved and the method of construction of the figure are the same as those for the construction of a similar figure for Esthwaite Water (see § I, Fig. 14 and relevant discussion). Concentrations of the substances concerned are plotted for comparison on a common scale of mg.-equiv./l. The differences between the equivalents of conductivity, alkalinity, iron etc. are not plotted in Fig. 21 as was done in Fig. 14, as relative changes are sufficiently striking without this. As in Esthwaite Water, the difference between 'total salts' and alkalinity decreased after reduction of the mud surface, and the same explanation for this decrease may be suggested, namely, that it may be partly due to the reduction of

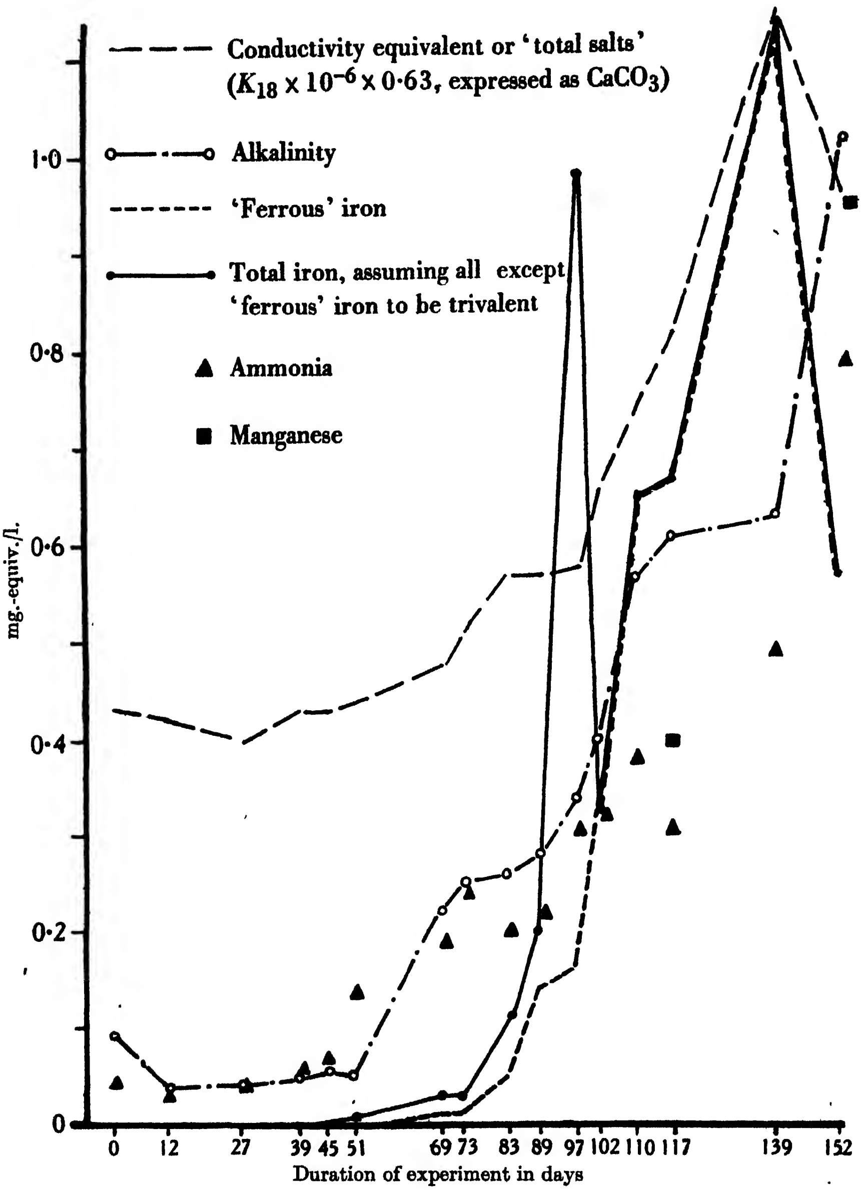


Fig. 21. 'Total salt' and 'excess base' content of the anaerobic tank, compared with the respective contributions of iron, ammonia and manganese. All concentrations expressed as mg.-equiv./l.

sulphate or partly to the inclusion of some un-ionized basic material (e.g. ferric hydroxide) in the alkalinity value.

It is in the comparison of the equivalents of total alkalinity and the other bases that the main difference between Esthwaite Water and the anaerobic tank appears. In the former case (Fig. 14), total iron (even when considered to be trivalent and wholly active in the alkalinity titration) plus ammonia only made up a portion of the total alkalinity, the residue being attributed to other bases. In the anaerobic tank (Fig. 21) ammonia alone was almost equivalent to total alkalinity, leaving iron, manganese and possibly other bases unaccounted for. This considerable discrepancy cannot be explained satisfactorily without further research. It may, however, be suggested that a large part of the iron may be in complex form and not included in the alkalinity value. The same may also be true of manganese. Even so, if it is assumed that ammonia is fully ionized, this does not leave much residual alkalinity as evidence for the presence of other bases. It is possible that, in confined, base-poor systems of this kind with no outside source of supply of monovalent and divalent bases, the available bases are bound by bacteria or in other ways. Another difficulty lies in the way of the assumption that the iron is in complex form. This is the strong positive colour reaction which was obtained with α-α'-dipyridyl, which is usually considered to be a specific indicator of Fe^{++}. It is of interest in this connexion that Coolidge (1932), during the study of iron complexes of the iron-protein type in yeast, found that ferrous iron existed in un-ionized form, but gave a positive reaction with α-α'-dipyridyl. It is also of interest that the E_0 value (potential at which equal quantities of oxidized and reduced phase exist in equilibrium) of these complexes and also of artificial iron-albumin complexes was found to be about 0·2 V. at pH 7. This E_0 value, which is approximately the same as that observed for the iron systems in natural waters, muds and soils (Pearsall & Mortimer, 1939), is much higher than the E_0 of most better known iron complexes (e.g. iron pyrophosphate, E_0 – 0·6 V. at pH 7) and much lower than the E_0 of the inorganic $Fe^{+++} \rightarrow Fe^{++}$ system (0·75 V. at pH 4). Recent work on the chemistry of humus (Waksman, 1936) recognizes a lignin-protein complex as the essential constituent. The similar behaviour of iron-protein complexes (Coolidge, 1932) and iron complexes in natural muds, suggests that the latter may be essentially iron-humus complexes.

The behaviour of samples taken from the anaerobic tank during the latter part of the experiment provides further evidence of the difference between the state of the iron in these samples and in samples from the reduced hypolimnion in Esthwaite Water. On exposure to the air, the iron in lake samples was almost all precipitated as ferric hydroxide with a corresponding fall in conductivity and alkalinity. During a similar period of exposure to the air, precipitation did not occur in a reduced sample taken from the anaerobic tank at 110 days, but the colour was trebled and the alkalinity and conductivity fell slightly. Although this difference in behaviour cannot be explained, it may have been due to the 'protective' action on the ferric colloids of a higher concentration of organic matter in the water of the tank. A fuller explanation of the way in which the ferric iron was kept in 'solution' may throw light on problems of transport of iron in peaty waters and soils.

In a stimulating paper, Ohle (1937) has described phenomena associated with the colloidal properties of mud constituents, and has emphasized the importance of these properties in the control of the exchange of plant nutrients in lakes. In particular he has demonstrated the 'ampholytic' nature of the ferric hydroxide gel, which is electro-positive in acid and electro-negative in alkaline solution. Thus in the presence of CO_2 at pH 4, negatively charged phosphate ions added to ferric hydroxide gel were strongly adsorbed, although some of the iron went into solution. After raising the pH to 9 by the addition of calcium bicarbonate, a large part of the phosphate was liberated. This may in part explain the fundamental influence of the presence or absence of bases (calcium) on the degree of productivity in fresh water. In the water of base-poor humus lakes phosphate and other plant nutrients are adsorbed on iron gels which are themselves attached to electro-negative humus colloids. Hence productivity is low. It is possible that an essentially similar process occurs in the oxidized mud surface of other lake types, producing the adsorption effect described in the present paper. Ohle has also shown that in higher pH ranges, manganic ions, which begin to precipitate as hydroxide at pH 8, also exercise an adsorptive influence. In many cases the phosphorus cycle may be more closely coupled with the manganese cycle than with iron, especially if sufficient organic colloids are not present to 'protect' the iron from rapid precipitation and removal. Ohle's results and those in the present paper are sufficient to indicate the important part which colloid chemistry is destined to play in the study of lake 'metabolism'.

As a result of observations on the anaerobic tank it is now possible to define more closely the potential ranges within which the following reductions may be expected to occur in mud-water systems. These ranges in E_7 V. units are given below in brackets. The first potential given is that below which active reduction may be considered to have occurred in the water, i.e. where the fall in concentration was too rapid to be explained by diffusion into the mud. The second potential is that below which none of the oxidized phase could be detected in the water. Nitrate to nitrite (0·45–0·40 V.); nitrite to ammonia (0·40–0·35 V.); ferric complex to ferrous complex or Fe^{++} (0·30–0·20 V.); sulphate to sulphide (0·10–0·06 V.). The oxygen concentrations associated with these potential ranges in the anaerobic tank were approximately 4, 0·4, 0·1 and zero mg./l. respectively. In Esthwaite Water 1939 (see preceding section) it was observed that the first appearance of ferrous iron at 13 m. (1 m. above the mud) occurred at a potential between $E_7=0·3–0·2$ V. and was associated with an oxygen concentration of approximately 1 mg./l., a much higher concentration than that observed at the same stage in the anaerobic tank. It is possible that the conditions found in Esthwaite represent an unstable state due to mixing by eddy diffusion of water containing ferrous iron, and at a low redox potential near the mud surface, with water containing more oxygen from higher levels. This presupposes that ferrous iron is not oxidized instantaneously, a supposition which was justified by conditions found during mixing preceding the overturn, at which time ferrous iron was detected in water containing 8·4 mg./l. of oxygen.

(*To be continued*)

THE VEGETATION OF THE SESE ISLANDS, UGANDA

AN ILLUSTRATION OF EDAPHIC FACTORS IN TROPICAL ECOLOGY

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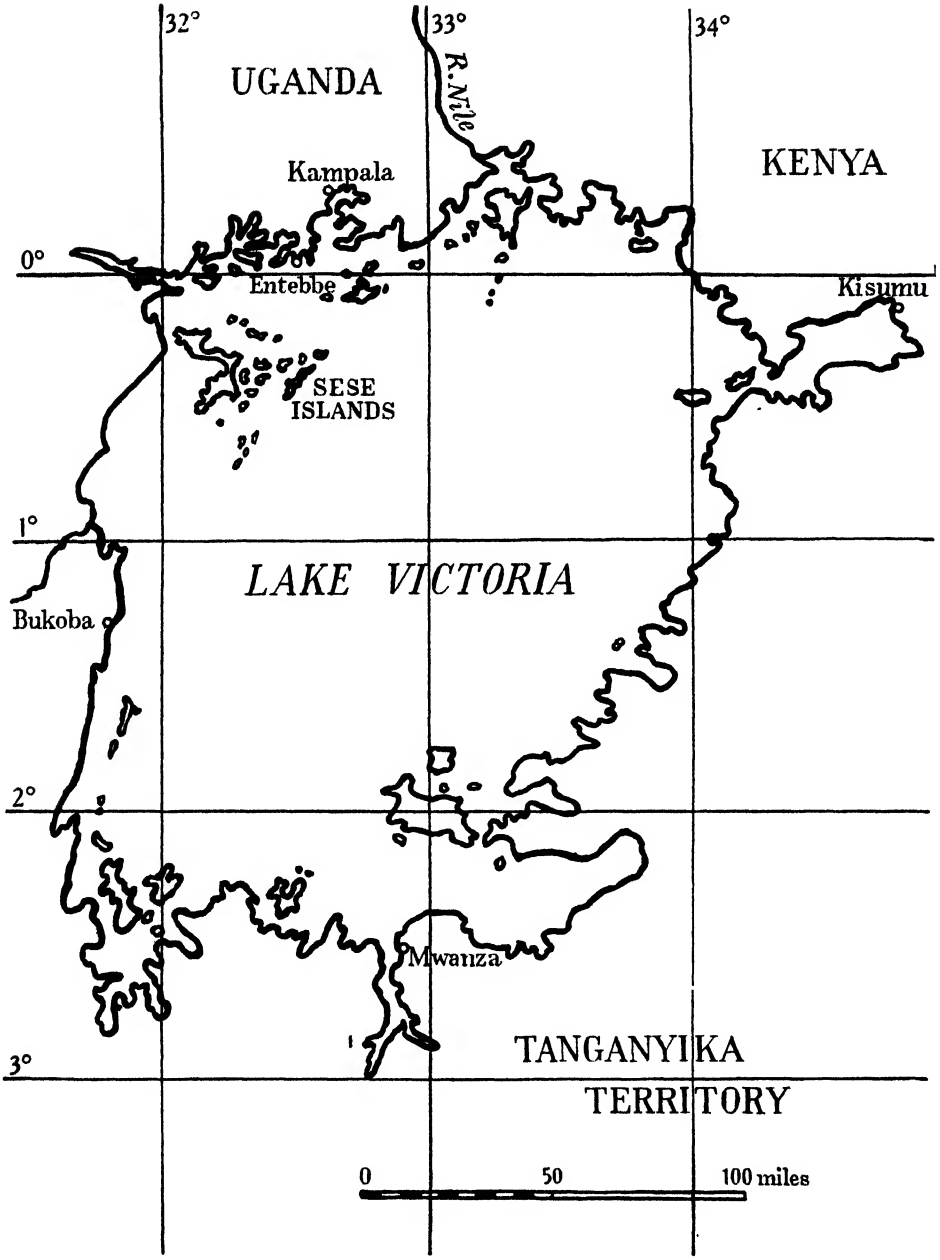
(*With Plates* 20–22 *and two Figures in the Text*)

Introduction

The Sese Islands form a group near the north-west corner of Lake Victoria, lying between latitudes 0° 10′ and 0° 45′ S. and between longitudes 32° and 32° 35′ E. The islands vary much in size, from Bugala, the largest, which is about 35 miles long, down to mere islets of rock; but all are narrow (even on Bugala no point is more than 3 miles distant from the lake) and all rise by gentle slopes to central ridges less than 100 m. above lake level (1120 m.). Beneath the surface of the ridges are sheets of ironstone, which have resisted denudation and which are responsible for the peculiar ringing sound of footsteps on the pathways.

At the end of the nineteenth century the islands carried a population of about twenty thousand people and large herds of cattle. The inhabitants, Basese, were a Bantu tribe, closely resembling the Baganda on the neighbouring mainland and were included in the Buganda kingdom; the shrine of the principal Muganda deity, Mukasa, was in the Sese Islands, and the Basese were regarded as powerful in witchcraft and had a reputation of being cannibals. Fishing was a great industry on the islands, for the people constructed magnificent canoes of planks sewn together with the fibre of the local raphia palm, *Raphia Monbuttorum* Drude, in which they travelled long distances although fierce storms sweep over the lake making the water as rough as the sea.

The people also were skilled herdsmen, having a long tradition of cattle keeping; on account of their wealth of stock they were subject to raids by other tribes, and there still exist the trenches and ramparts which were constructed for defence of some of the headlands. They also grew food crops, mostly sweet potatoes and bananas, and possessed many large trees of Robusta coffee, *Coffea canephora* Pierre, whose produce was exported to the mainland. On some of the islands there was great pressure on land: it was all under grassland or farms, all the original forest trees had been cut down and fuel was so scarce that tufts of a coarse grass, *Eragrostis blepharoglumis* K. Schum., were twisted tightly together for burning.


32°
33°
34°
UGANDA
R. Nile
KENYA
Kampala
0°
Entebbe
Kisumu
SESE ISLANDS
1°
LAKE VICTORIA
Bukoba
2°
Mwanza
3°
TANGANYIKA TERRITORY
0
50
100 miles

Sleeping sickness appeared in 1902 and swept through the islands, causing an enormous mortality; in some places the population was literally decimated, and the situation was so bad that in 1909 all the remaining inhabitants were removed to the mainland, out of range of the tsetse fly, *Glossina palpalis* Westwood, which was the vector of the trypanosome causing the disease. After the evacuation, the whole aspect of the islands rapidly changed and forest quickly covered all the farms, although the grassland altered little. Hale Carpenter (1920), who studied *Glossina* there in 1912–13, has described the islands, their climate and their fauna.

By 1920 the sleeping sickness was well under control and inhabitants were encouraged to return, but many people preferred to stay on the mainland and the total population of the islands now is only four thousand. It is hard to realize that so many people still live there, their farms and houses are hidden in the forests and from a distance there is little sign of human occupation except the canoes drawn up on the shores of the landing places. Many of the smaller islands are now uninhabited, except for the temporary camps of fishermen. Fishing is now the main industry of the islanders, who make a good living by the sale of smoked fish in the markets on the mainland.

When it is viewed from the lake, the vegetation of the Sese Islands exhibits a distinct pattern which, with slight variations, is repeated on all of them; the hillsides are covered with stretches of pale short yellowish grass, contrasting vividly with the strips of dull dark green forest along the tops of the hills; in some places there is also a narrow strip of forest beside the shore and, less frequently, the forest may be continuous in valleys from lake-shore to hilltop (Pl. 20, phot. 1). If the weather is fine and the water is blue in the sunshine, the Sese scenery is idyllic; in bad weather, when the lake is churned into a grey swell and all the colours are dulled, the islands are peculiarly depressing.

THE PLANT ASSOCIATIONS ON THE SESE ISLANDS

(1) *Aquatic vegetation*

The water of the open lake is clear and is free from any large floating water plants; on the exposed sides of the islands, those facing the open lake to the south and east, the waves sometimes are so large that any floating plants would be washed away and therefore clear water extends up to the shore, but, where the water is less disturbed, there are distinct zones of aquatic vegetation. The first plant association is seen in water about 1·75 m. deep and consists of floating grasses, known in Sese as 'Ndago', usually a mixture of *Paspalidium geminatum* Stapf and *Panicum repens* L. The habit of these species is similar, with stems up to 2 m. long in the water and with a few leaves and the inflorescences projecting about 50 cm. above the surface. This zone is of considerable economic importance to the islanders, for it is the haunt of abundant small fish locally known as 'Nkeje', which are caught and dried for export.

In more shallow water, about 1 m. deep, there is usually a belt of rushes rooted in the bottom, whose stiff erect stems project about 75 cm. above the water: *Eleocharis* sp. sometimes is dominant, while in other places *Scirpus corymbosus* Roth. is abundant. On the landward side of the rushes there are frequently large masses of reeds, *Phragmites mauritianus* Kunth., a species with greyish leaves and stems up to 2 m. high. When these reeds are near frequented landing places, often they are populated by colonies of small yellow weaver birds which are absent from the reeds growing on deserted stretches of shore.

In very shallow water on the edges of the forest the Ambatch, *Herminieria elaphroxylon* Guill. & Per., is common, growing into large shrubs up to 6 m. high, whose thick pithy spreading branches are a favourite haunt of the cormorants and divers, grotesquely perched with wings outspread to dry them. The light green leaves and large orange-yellow flowers of the *Herminieria* form a vivid contrast to the dull dark green of the forest behind, and it constitutes the landward zone of the water plants.

In landlocked bays, where the water is even less disturbed than on the leeward side of the islands, there are many characteristic floating water plants. In such places *Azolla nilotica* Desm. often forms a dusty red film over the water; the vivid green rosettes of *Pistia Stratiotes* L. are abundant; *Limnanthemum Whytei* N.E.Br., with leaves like those of a small water lily and a succession of bright yellow flowers, is common; and *Jussieua diffusa* Forsk., buoyed up by its inflated white roots, is frequent. Two species of *Nymphaea* have been found among the Sese Islands: *N. capensis* Thunb., with reddish leaves and lilac flowers, is the more common, while *N. lotus* L., with larger serrate leaves, is not infrequent although less noticeable, for its large white flowers are open only at night and in the early morning. The long strands of *Ceratophyllum demersum* L. are abundant below the surface of the water. Papyrus, *Cyperus Papyrus* L., also is found in the landlocked bays in considerable amount: for example, in the large bay on Fumve Island it forms a wide belt, the haunt of numerous sititunga, a species of antelope interesting on account of its aquatic habitat.

(2) *Lakeside Forest*

The nature of the shore varies according to the configuration of the land. On exposed places it often consists of rock more or less tree-clad down to the water level; sometimes narrow tongues of gently shelving slabs of ironstone project into the water, and such spots are a favourite haunt of crocodiles, which are abundant around the islands; most of the sheltered bays have narrow beaches of fine white sand. Formerly, when the islands were densely populated and the trees and shrubs were cut for fuel, in most places the grassland stretched right down to the shore, but at the present time there are long strips of lakeside forest around each island. It is noteworthy that where the shores are rocky there is usually a belt of forest: even small islets of rocks projecting only a few feet above the water are usually completely covered with trees with little undergrowth. The slabs of ironstone are bare except for the tree roots creeping over them down into the water. On rocky headlands which are composed of horizontal sheets of ironstone or of rugged outcrops of quartzite and on other exposed shores, the trees often grow right down to the edge of the water, overhanging it for some distance (Pl. 20, phot. 2). In sandy bays, the grassland usually stretches down to the lake, but even in such places the forest is slowly extending along the shore.

In some very sheltered spots there is a belt of *Raphia Monbuttorum* growing on the swampy ground between the lake and the forest; this quick-growing and short-lived palm is common in swamps on the mainland of Uganda. *Phoenix reclinata* Jacq., a palm which is abundant on the edges of swamps in most parts of Uganda, is absent from many of the Sese Islands although it is common on Buninga, the western end of Bugala Island where, as mentioned below, the soil is different from that of the rest of Sese. In sheltered places the edge of the forest often consists of a dense mass of *Alchornea cordifolia* Muell. Arg. rooted just above the water and extending to a height of 8 m.; often the tangle of branches is so thick that it is impossible to penetrate except along the low tunnels made by the hippopotami when they come out of the lake at night and pass through the forest to graze on the pastures beyond. *Bridelia micrantha* Baill. in some places is abundant in admixture with the *Alchornea*, and *Dissotis segregata* Hook. f., a rounded shrub 1·5 m. high, is often found outside the forest edge between trees and water.

The dominant species of the lakeside forests is *Uapaca guineensis* Muell. Arg., a quick-growing tree attaining a height of about 20 m. with a rounded crown of large dark leaves; the most striking character of this species is the great development of prop roots arising from a height up to 5 m. on the trunk and extending over a considerable area. When the lakeside forest is viewed from the top of the hills often it is seen to be a continuous band of the dull dark rounded crowns of *Uapaca*; in other places the canopy is broken by the flat crowns of *Piptadenia Buchananii* which are higher than those of *Uapaca* and different in colour—when the leaves are young, they are tinged with brown and when they are fully expanded, they are of a much lighter green than those of *Uapaca*.

In exposed places *Piptadenia Buchananii* is more common than on the sheltered sides of the islands: in some patches of forest it is the dominant tree (Pl. 21, phot. 3). The two species are so dissimilar in appearance—the prop root system, the brown bark, the rounded crown of large leathery dark leaves of *Uapaca* are in violent contrast to the buttress roots, the grey bark and the flat crown of bipinnate leaves of *Piptadenia*—that it is strange that they should be in association; these two species comprise 90 % of the trees of the lakeside forest. One other species is characteristic of this zone, *Ficus Drewei*

Hutch., whose very spreading horizontal branches and glossy leaves make it a conspicuous tree when viewed from the lake. Other tree species such as *Maesopsis Eminii* Engl. do occur, especially in the hollows where the soil is relatively good and which were under cultivation when the islands were densely populated, but such trees are much more abundant in the hill-top forests on land which formerly was all under farms.

The climax of the Lakeside Forest may be seen in the Towa Forest on Bugala Island, where the land sloping gently down to a landlocked bay is too wet for cultivation and therefore remained under forest when there was a large population on the islands; the slopes around, however, were covered with farms and the forest has now spread over them. In the lower, wetter, parts of the Towa Forest, *Uapaca guineensis* is the only tree species and forms a dense canopy of leaves about 20 m. above the ground: below this canopy may be seen its smooth red-brown trunks, up to 1 m. in diameter, branching into the mass of large prop roots. Very few species seem to grow under a dense stand of *Uapaca*; the intensity of light is greatly reduced, and it is probable that few other plants can compete with its root system. Therefore in denser parts of the Towa Forest there is no undergrowth of small trees or large shrubs although the stems of a few lianes may be seen.

Large areas of the thicker parts of the Towa Forest and of lakeside forests on other islands are covered with a pure stand of *Lasianthus seseensis* Taylor, a small erect shrub growing to a height of 1·5 m., with dull dark leaves and axillary clusters of small pinkish flowers which are followed by porcelain-blue berries about 1 cm. in diameter. This species, which is dominant over much of the forest on Sese, appears to be endemic to the islands, for it has not been recorded from any of the wetter forests on the mainland.

In the densest part of Towa Forest there are in the undergrowth few flowering plants other than *Lasianthus seseensis*, and the mosses are the only other important plants in the association. *Pilotrichella pilifolia* Dix. and *P. cuspidata* Broth. are abundant in festoons on any low branches: *Reynauldia Hoehnelii* Broth. and *Rhizogonium spiniforme* Broth. are common on the prop roots and on fallen trunks of *Uapaca*; while *Fissidens rugifolius* Dix., a species recorded only from the Sese Islands, forms a close cover over small termite hills on the forest floor.

Wherever there is a break in the canopy in the Towa Forest, there is an abundance of ferns, ranging in size from the dwarf filmy-fern *Trichomanes bipunctatum* Poir., which is common in the moister parts, up to tree-fern *Cyathea Deckenii* Kukn. which forms handsome groups with trunks up to 6 m. in height in some of the swampy hollows. *Marattia fraxinea* Sm., another majestic fern with fronds up to 3 m. long and 1 m. wide, is less frequent and the most common terrestrial ferns are *Pteris atrovirens* Willd., *Asplenium splendens* Kze., *Bolbitis gemmifer* C. Chr. and *Nephrolepis biserrata* Schott. The last is widely distributed on the Sese Islands in thick belts near the edges of the forests. The large clumps of *Polypodium irioides* Poir. render it one of the most obvious of epiphytic ferns, but *Asplenium Mannii* Hook., *A. Sandersonii* Hoch, *Acrostichum* spp. and *Loxogramme lanceolata* Pr. are also very common on the trunks and branches of trees.

In addition to the mosses and the ferns, the epiphytic flora of the lower part of the Towa Forest comprises *Peperomia bagroana* C.DC. and *P. Holstii* C.DC., which are both abundant. The most interesting epiphyte is *Medinilla* n.sp. (Th. 1358, 3026), which has not been found outside this area; it is a shrub with spreading drooping branches up to 1·5 m. long, bearing small crimson flowers in clusters at the nodes and having long fleshy roots, about 3 cm. in diameter, which creep along the bark of trees under the layers of moss.

The *Uapaca guineensis–Lasianthus seseensis* association, described above, is typical not only of the lower parts of the Towa Forest but also occurs in many other sheltered moist lakeside forests on other islands. It covers a large part of Fumve. The higher part of the Towa Forest, and most of the other lakeside forests, comprise a much greater variety of tree species, although *Uapaca* usually is dominant. As mentioned above, *Piptadenia Buchananii*, *Ficus Drewei* Hutch., and *Maesopsis Eminii* are common; *Conopharyngia Holstii* Stapf is frequent; so is *Musanga Smithii* R.Br., which, like *Uapaca guineensis*, often has a well-marked development of prop roots but which in Uganda never produces the masses of suckers so characteristic of this species in West Africa. Other tree species occasionally encountered are *Polyscias fulva* Hutch. & Dalz., *Baikiaea minor* Oliv. and *Monodora Myristica* Dun.; the succulent *Euphorbia Teke* Schweinf. is common, growing into the form of a small tree about 6 m. in height.

Many species of shrubs also are found in the more mixed lakeside forests: *Dracaena fragrans* Ker. Gawl. is very common, and the larger *D. Steudneri* Schweinf., so common in the secondary forests of the mainland, also occurs on Sese. The coffee-like *Tarenna pavettioides* Sim. is common, growing to a height of 3 m., while one true coffee, *Coffea eugenioides* S. Moore, has been found in two or three localities on the islands. In many places, a greater part of the undergrowth is made up of members of the Marantaceae; *Clinogyne Hensii* K. Schum. sometimes covers considerable areas, forming a mass of leaves about 1·5 m. high, while other common species are *C. ugandensis* K. Schum., *Hybophrynium Braunianum* K. Schum. and *Marantochloa ugandensis* K. Schum.

In places where there is a break in the canopy of the mixed lakeside forest large terrestrial ferns often grow in abundance; the more common species are *Nephrolepis biserrata* Schott., *Dryopteris protensa* C.Chr., *Lonchitis Burrori* Mett. and *L. glabra* Bary. Two plants are characteristic of the ground layer in the mixed lakeside forests: first, *Palisota Schweinfurthii* C.B.Cl. with big rosettes of fleshy leaves: and secondly, the small creeping herb *Geophila hirsuta* Benth., whose orange berries contrast vividly with the dark leaves forming a close thick cover over the ground.

Lianes are often abundant: *Landolphia florida* Benth. is very frequent and *L. owariensis* Beauv. has been reported; *Alafia lucida* Stapf and *Clitandra orientalis* K. Schum. are common; *Carpolobia alba* L. makes a striking display when it is in blossom. It was mentioned above that epiphytic ferns and mosses were common in the denser parts of the lakeside forests; few orchids are found in such parts, but near the edge of the forest or by open glades where the trees have made long horizontal branches, orchids are locally abundant; *Polystachya polychaete* Kraenzl., *P. tesselata* Lindl. and *Tridactyle* sp. are common, while *Bulbophyllum platyrachis* Schlecht. also occurs.

In many places the lakeside forest stops abruptly, from the dense shade and abundance of epiphytes one passes immediately into the short open grassland; in other places there is a belt of scrub outside the forest, although it is seldom so marked as that around the hilltop forest. Some very interesting species, however, do occur near the forest edge: the fern *Gleichenia linearis* C.B.Cl., which has been reported nowhere else in Uganda, is frequent in this position on the Sese Islands, growing into a dense mass 1·5 m. high of light yellow-green stems and leaves: and on Bukasa island *Gardenia imperialis* K. Schum., a small erect tree with fragrant funnel-shaped flowers 10 cm. long, also is common. This species has been found in Uganda only on the Sese Islands and at Nabugabo on the adjacent mainland.

(3) *Grassland*

Between the two belts of forest—that beside the lake and that on the ridge of the islands—the slopes are covered with short grassland; in some places this grassland sweeps over the top of the islands, while in others, especially in sheltered hollows, there is a continuous belt of forest from the lakeside to the top of the hill. The light colour of the grassland is due to the fact that *Loudetia kagerensis* C. E. Hubbard, is the dominant species; this grass grows in small tufts about 75 cm. in height with narrow leaves and a paniculate yellow-brown inflorescence; the stems are thin, swaying in the slightest wind and giving to the grassland its characteristic moving sheen. *L. kagerensis* is also common in some other parts in the west of Uganda where the soils are very sandy like those of the Sese Islands. Several other grasses are common in admixture with the *Loudetia*; *Eragrostis chalcantha* Trin. is abundant, and its small tufts are most evident after the grassland has been burnt for it starts into growth quickly and flowers before the *Loudetia*; *Ctenium concinnum* Nees var. *indutum* Pilger and *Andropogon Dummeri* Stapf are widespread on the islands and in some places are important constituents of the grassland. Where the ground has been disturbed—for example, beside the paths and on anthills—and in rocky places, *Eragrostis blepharoglumis* K. Schum. is the dominant grass, growing in large tufts, with coarse hard leaves (Pl. 21, phot. 3). In some places, especially on top of the ridges near the forest, *Hyparrhenia diplandra* Stapf is abundant; this is a much taller grass than the *Loudetia* and appears to require better soil, for it becomes dominant near cattle kraals; it is also noteworthy that tree seedlings, especially those of *Anthocleista Schweinfurthii* Gilg., may be seen growing in stretches of *Hyparrhenia diplandra*, although they are absent from the main areas of grassland where *Loudetia* is dominant.

Most of the soil of the Sese grassland is sandy, very deep, porous and rapidly drained. In a few hollows on the grassland where a layer of ironstone prevents good drainage, swamp results, and the *Loudetia kagerensis* is replaced by *L. phragmitoides* C. E. Hubbard, a much more vigorous species growing to 2 m. in height, which is frequent in swampy grasslands throughout the west of Uganda. Near the Towa Forest there is a large stretch of swamp at lake level covered with *Miscanthidium violaceum* Robyns, a grass dominant in many swamps in the western parts of Uganda (Eggeling, 1935); this species forms large clumps of long sharp-edged glaucous leaves (from which it derives the Luganda name *Kisalu* = it cuts) and large pink panicles rising to a height of 3 m., so that even from a distance its appearance contrasts vividly with the short yellow-brown stretches of *Loudetia kagerensis*.

Near the top of the slopes there are often outcrops of ironstone (Pl. 20, phot. 1), whose rough red-brown surface is encrusted with grey lichens, e.g. *Parmelia* sp., while there are often spreading plants of *Cyanotis* sp. and *Aeolanthus repens* Oliv. rooted in the cracks. In the shallow soil on the upper side of these outcrops there is often a stretch of short tuft in which the dwarf yellow *Kyllingia chrysantha* Schum. and the small tufted mauve-flowered *Ilysanthes trichotoma* Urban are abundant; in places where there is seepage of water over the surface of the rock the small yellow-flowered *Utricularia erecta* Kam. may be found.

A few other species of dicotyledons are widespread throughout the grassland although they are seldom present in large quantity: among them may be mentioned *Sesamum angustifolium* Engl., *Tephrosia barbigera* Welw. and *Lightfootia abyssinica* Hochst. var. *tenuis* Oliv. *Indigofera capitata* Kotschy, a compact subshrub about 50 cm. high, is abundant in some places; branches of this species are sometimes placed by the Basese in coffee bushes at the time of flowering in order to encourage the setting of a large crop of fruit, but it is difficult to see a reason for this belief, as the umbels of dull flowers do not seem to be very attractive to bees. Another widespread plant in the grassland is the small scarlet-flowered form of the semiparasitic *Striga asiatica* O. Kze., which like its host *Loudetia kagerensis* is often found on poor sandy soils of the mainland of Uganda.

In places where numbers of cattle are kept in kraals built on the grassland, the grazing and manuring have greatly altered the composition of the herbage. The *Loudetia kagerensis* is decreased in amount, while the *Hyparrhenia diplandra* is greatly increased and so is *Eragrostis Mildbraedii* Pilger; *Axonopus compressus* P. Beauv. is common in such places and *Digitaria longiflora* Pers. frequent. On the actual sites of abandoned kraals, where the ground has been consolidated and manured, *Paspalum Commersonii* Lam. is the dominant grass; one patch of *Cynodon Dactylon* Pers. was found also on a kraal site, the only instance in which this grass, which is abundant on the mainland, was noticed on the Sese Islands.

The landing places on the shores of the islands are covered with a short close turf quite different from that of the grassland above. *Eragrostis Mildbraedii* is often dominant near the edge of the water, growing in admixture with *Panicum repens* and *Hemarthria natans* Stapf: in the same zone of wet soil *Torenia parviflora* Benth., *Lindernia diffusa* Wettst. and *L. Whytei* Skan are common; sedges are abundant, including *Pycreus Smithianus* C.B.Cl., *Rhynchospora corymbosa* Britt. and *Lipocarpha senegalensis* T. & H. Dar. On the higher ground a few feet above the level of the lake *Axonopus compressus* is often the dominant grass, mixed with *Digitaria longiflora* and *Brachiaria decumbens* Stapf. As in the case of kraal sites, so also at the landing places, the treading and manuring of the soil (quantities of fish are landed and cleaned at some landing places) has produced a turf quite different from the sparse tufted grassland on the hills, and it is obvious that this turf is much more palatable than the general grassland, for it is closely grazed by hipppotami.

Colonization of the grassland by the spread of the forests is a slow process on the Sese Islands, but where anthills occur the process is greatly accelerated and the anthill colonies are one of the most interesting features of the vegetation of the islands. The Sese anthills are not very large, being up to 3 or 4 m. in diameter and 2 m. high, and in colour they are a little redder than the ordinary grassland soil. Newly formed anthills are bare, but on older ones there are tufts of grasses, especially *Eragrostis blepharoglumis* and *Hyparrhenia diplandra*, which, as mentioned above, denote soil somewhat richer than that of the average Sese grassland. As the anthill grows older other plants appear, not on the hill itself but on the ring of bare ground around the base; first, *Volkensia Duemmeri* B. L. Burtt, a mauve-flowered subshrub up to 2 m. in height; and secondly, *Harungana madagascarensis* Lam., a large spreading shrub up to 8 m. in height and 10 m. in spread. In the shade of the *Harungana* there soon appears an undergrowth of *Renealmia* sp. and *Aframomum sanguineum* K. Schum.; in the next stage the seedlings of trees appear, *Maesopsis Eminii* is the most common, while *Sapium ellipticum* Pax is frequent and *Vitex keniensis* Turrill occasionally occurs. Therefore in a few years the anthill is surrounded by a clump of trees with an undergrowth of Zingiberaceous herbs; other species soon appear, notably the scandent shrubby *Mussaenda arcuata* L. and the strong-growing liane *Landolphia florida*. The *Volkensia* and *Harungana* persist in a zone around the outside of the colony and, as the trees increase in size, the shrubs spread out into the grassland (Pl. 21, phot. 4). These anthill colonies are especially numerous near the lakeside forest, and as they increase in size they may become merged with each other and with the forest; but even when the covering of trees becomes continuous, the method of spread is still evident, for the anthills persist with the larger specimens around them. Griffith (1938) has pointed out that in Uganda the soil of anthills sometimes is richer in plant nutrients than is the land around, but he suggested that the physical effect of the mound—for example, by affording space for plants out of the range of fires—is the most important factor in stimulating plant growth. The fire factor does not seem to be of great importance on the Sese Islands; the sparse thin *Loudetia kagerensis* does not burn with the intensity of larger grasses, and where sheltered by the forest there may be seen small patches of grassland in which the tangled mass of old stems shows that they have not been touched by fire for years, and which, nevertheless, are not being colonized by tree seedlings. Furthermore, on the Sese Islands the woody species do not grow on the anthill itself but near the base, close to the grassland; tests made with a field set (Spurway, 1938) have shown that the soil at the base of an anthill is almost always richer than the ordinary grassland soil, and it is highly probable that the extra supply of plant nutrients renders possible the growth of trees instead of grasses.

(4) *Upper Forest*

Mention has been made of the layer of ironstone near the tops of the hills, which has greatly influenced the topography of the islands; this layer, in addition to retarding denudation, has prevented the loss of plant nutrients by leaching, and in many places the percolation of water is so reduced that the land is quite swampy, for example, the path along the flat top of Bukasa Island is under water for much of the year. On account of the diminution of leaching the relatively shallow upper soils are much more fertile than the deep sandy soils of the hillsides; when the islands were densely populated these hilltops were all under farms, and the pressure on land was so great that soil was carried and spread over layers of horizontal ironstone in order to increase the area for cultivation; the inhabitants were forced to undertake this labour because they had found that no agricultural crops could be raised on the grassland soils. When the islands were evacuated, the farm land became covered with dense secondary forest and, while many farms have been made since the return of the Basese, large areas of the forest remain uncleared.

Although the most important tree species of the lakeside forests, *Uapaca guineensis* and *Piptadenia Buchananii*, occur on the upper forests, yet they are seldom dominant over large areas, and there are great differences between the aspect of the upper and lower forests. The upper forests contain a much greater variety of tree species: *Maesopsis Eminii* is the most abundant and often is subdominant, but many others are common—for example, *Pycnanthus Kombo* Warb., *Pseudospondias microcarpa* Engl., *Polyscias fulva*, *Musanga Smithii*, *Conopharyngia Holstii*, *Anthocleista Schweinfurthii*, *Antiaris toxicaria* Lesch., *Canarium Schweinfurthii* Engl. and *Erythrina abyssinica* Lam. The raphia palm, *Raphia Monbuttorum*, also is very common throughout the upper forest, especially in the wetter parts; in a very waterlogged part of the upper Bukasa forest, *Macaranga monandra* Muell. Arg. is locally dominant (Pl. 22, phot. 5).

The shrubs of the lakeside forests also grow in the upper forests—*Tarenna pavettoides*, *Dracaena Steudneri* and *Euphorbia Teke* are very common. There is a wealth of climbers, and in some places all the trunks of the trees are covered with *Culcasia sendens* P. Beauv., while *Piper guineense* Sch. & Thon. is abundant; *Basella alba* L. is common, and on Bukasa Island *Passiflora edulis* Sim. has become naturalized and is abundant in the forests; in clearings there is often a mass of the scandent *Scleria Barteri* Boeck., whose sharp-edged leaves are a great hindrance to progress.

The ground cover is similar to that of the lakeside forests—the various species of Marantaceae and also *Palisota Schweinfurthii* are especially common. Three species of grasses typical of the wetter Uganda forests are found in the upper forests of the Sese Islands—*Leptaspis cochleata* Thwaites is dominant in some places: *Streptogyne gerontogaea* Hook. f. is present, but seldom in quantity; while in clearings and beside paths the large clumps of *Setaria caudula* Stapf are abundant. Another characteristic forest plant is the terrestrial orchid *Eulophia euglossa* Rchb. f. which occurs on several of the islands, producing long racemes of small rather inconspicuous flowers.

Epiphytic orchids are much more abundant in the upper forests than in the lakeside forests, as a much higher proportion of the trees have rough bark suitable for their growth; incidentally, it is interesting to note that the specimens of *Erythrina abyssinica* seen on the Sese Islands have relatively smooth thin bark in comparison with the thick rough bark of the trees growing in savannah forests on the mainland. No doubt this is a climatic effect. A species of *Tridactyle* with narrow leaves and inconspicuous flowers is the most abundant orchid on the Sese Islands, for there is scarcely a single large tree of *Maesopsis Eminii* or *Canarium Schweinfurthii* on which it is not growing. *Polystachya polychaete* and *P. tessellata* also are common; on the small island of Bubekke, *Angraecum infundibulare* Lindl., whose large solitary white flowers render it one of the most decorative epiphytic orchids of Uganda, is abundant.

Ferns also are abundant in the upper forest, both terrestrial and epiphytic, the species being mostly the same as those of the lower forests: the large clumps of the epiphytic *Polypodium irioides* Poir. and the smaller creeping *P. lycopodioides* L. and *P. scolopendria* Burm. are especially noticeable. The luxuriant growth of epiphytes and of stem climbers, especially *Culcasia scandens*, give to the upper forests a very 'tropical' appearance, which is in violent contrast to the short open grassland near by. Of course these Sese forests are secondary, and therefore it is only to be expected that they would exhibit this tangled mass of vegetation which is very different from most virgin tropical forests where the canopy of the trees is so thick overhead that the vegetation near ground level is sparse and open.

The transition between upper forest and grassland is usually less abrupt than the sharp edge of the lakeside forest, for there is often a zone of scrub outside the upper forest. Several species are abundant in this scrub, for example *Coleus shirensis* Guerke, *Smithia Kotschyi* Benth. and *Clappertonia ficifolia* Decne; members of the Melastomaceae are very characteristic of the forest fringes, *Dissotis Brazzaei* Cogn. is very common, *D. segregata* is frequent, and the small procumbent *D. decumbens* Triana is widespread. Two species of ferns, *Pteridium aquilinum* (L.) Kuhn. and *Gleichenia linearis* C.B.Cl., are typical of this forest edge and *Lycopodium carolianum* L. is common; on Bukasa Island *Cyathea Dregei* Kze. is locally common, an interesting occurrence as the species has been reported only from one other locality in Uganda, in old iron workings on hills of the Toro district (Eggeling, 1939) at a distance of 200 miles from the Sese Islands.

(5) *Farms*

The upper forest almost invariably appears to be a continuous sheet of trees when it is viewed from a distance, but on the inhabited islands large clearings have been made for farms, and the trees on the outside of the forest have been left untouched in order to give some protection from the violent winds which sweep over the islands. When the forest is cleared the undergrowth is cut and burnt around the trees in order to kill them, but large specimens of some species are often retained, especially *Canarium Schweinfurthii*, *Maesopsis Eminii* and *Antiaris toxicaria.* Many of these trees have a relatively short trunk and wide low crown on the Sese Islands, instead of the tall trunk produced when they have grown in dense natural forest; none of them have root systems which prevent good crop production near them, although other Sese trees such as *Uapaca guineensis* and *Piptadenia Buchananii* make such strong roots that no agricultural crops will grow in their vicinity and such trees are never left on farms.

The main food crop on the Sese Islands is the sweet potato, *Ipomoea Batatas* Lam., grown in mounds in large plots; another important root crop is cassava, *Manihot utilissima* Pohl., which is regarded as a food reserve and is planted on land from which successive crops of sweet potatoes have been taken and whose fertility therefore has diminished; small plots of rice, *Oryza sativa* L., are sometimes planted and beans, *Phaseolus lunatus* L., are commonly grown. Large woody cuttings of *Ficus Thonningii* Bl. are planted on the farms to grow into trees whose bark is used to manufacture barkcloth; and small amounts of other food crops such as taro, *Colocasia esculentum* Schott, and sugar-cane, *Saccharum officinarum* L., are grown. Banana gardens are common around the dwellings, but are not so large as on the mainland, for the Sese bananas are almost entirely of the types known locally as *Mbide*, varieties of *Musa sapientum* L., which are used for beer making, and there are few clumps of the *Matoke* varieties, *Musa paradisiaca* L., which are used for food. Bananas are very responsive to the degree of soil fertility, and it is noteworthy that the Sese bananas, with the exception of those on one or two farms which have been given good dressings of cattle manure, are not nearly so strong in growth as those of the mainland.

Coffee is the only export crop, for there is a long tradition in the culture of *Coffea canephora* Pierre, Robusta coffee, on the islands, and plots exist in which the trees are known to be all about 70 years old; one magnificent tree, whose trunk was a metre in circumference, died at an age of over 120 years. These old coffee trees growing near homesteads, on land which had been well manured with household refuse, remained vigorous in the secondary forest which grew up when the islands were abandoned and still produce good crops; yet when plots of coffee are planted away from the houses they have a very short useful life, unless there is heavy overhead shade. There is now little expansion in the export of coffee from the islands because the majority of people make a good living out of fishing, and there are so many drawbacks to agriculture on the Sese Islands—the soils are not rich, the damp climate stimulates rapid weed growth and the natural fauna is responsible for much damage to crops: old fishing nets are hung around the farms to keep out the grey monkeys which abound on the islands, and barriers of logs are made to stop the hippopotami.

The first weeds to appear on farms are ephemeral grasses, especially *Setaria aequalis* Stapf, *Digitaria velutina* Beauv. and *Eleusine indica* Gaertn.; after these quick-growing grasses there often appears a mass of annual Composites, *Ageratum conyzoides* L., *Bidens pilosa* L. and *Senecio abyssinicus* Sch. Bip. Two perennial weeds are of great importance—*Digitaria scalarum* Chiov., a 'couch grass' spreading rapidly by rhizomes, and *Commelina nudiflora* L., whose succulent stolons can only be destroyed by burying them, for there is never a sufficiently long dry spell on Sese for them to be dried in the sun.

Resting land soon becomes covered with a tangled mass of coarse herbaceous and subshrubby plants such as *Leonotis nepetaefolia* R.Br., *Triumphetta tomentosa* Bojer, *Aspilia* sp., *Brillantaisia Eminii* Lindau, *Indigofera arrecta* Hochst., and *Cassia Kirkii* Oliv. (Pl. 22, phot. 6). Intermixed with these plants are many grasses which do not occur in the natural grassland of Sese—*Panicum maximum* Jacq., *Panicum trichocladum* Hack., *Setaria sphacelata* Stapf & Hubbard and *Setaria pallidifusca* Stapf & Hubbard; on patches of the better soil there are large clumps of *Pennisetum purpureum* Schum., elephant grass, but this species does not become dominant over such large areas as on the mainland. The scrub association later is replaced by still taller plants; in some places thickets of *Smithia Kotschyi* appear, and such land is avoided when new farms are made, as it is said to be infertile; in other places tall masses of *Aframomum sanguineum* spring up and these in turn are replaced by secondary forest.

(6) *The vegetation of Buninga*

In the description of the soils of the Sese Islands it is mentioned that Buninga, the western part of Bugala, is on rocks of the Basement Complex; in this area there are stretches of sandy soil, covered with *Loudetia kagerensis*, intermixed with patches of forest. The soil of the forest areas is different from any seen elsewhere on the Sese Islands—it is a heavy brown loam, over a subsoil of yellow clay. In these forests *Spathodea nilotica* Seem. is abundant, although it is rare on the rest of the Sese Islands; *Acanthus arboreus* Forsk. is common at the edge of forests and *Phoenix reclinata* is abundant beside the lake. All these species are abundant on the mainland of Uganda, and their occurrence in Buninga, together with their absence from the rest of the islands, seems to show that the soils of Buninga more closely resemble those of the mainland than the soils of the remainder of the Sese Islands.

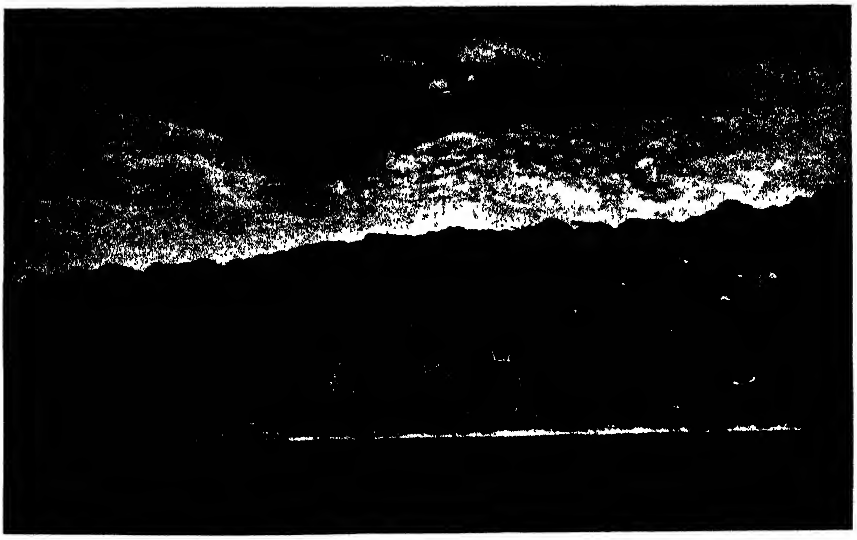
THE SOILS OF THE SESE ISLANDS

The islands (with the exception of Buninga) are situated on the Karagwe Ankolean system, consisting of sedimentary deposits which were leached when they were laid down; owing to the heavy rainfall, the soils derived from these rocks have again been leached and therefore they are relatively poor, as shown by the analyses given in Table 1.

These analyses are taken from those which have been made by the Chemical Section of the Uganda Department of Agriculture, and the results are corroborated by many observations on available nutrients made by Spurway's system (1938). Samples A to D represent the types of soils which occur from the base to summit of the slope on Bugala island; samples E and F are representative of good and bad farm soils near by; sample G is from a stretch of *Hyparrhenia diplandra* on Bukasa island; sample F is included to represent typical soil of the elephant grass areas of the mainland.

Samples A and B were taken near each other, one inside and one outside the forest near the lake, and samples C and D were taken in close proximity near the edge of the forest at the top of the slope. Comparisons between each pair show that the forest soils are no richer in phosphates than those of the grassland, but that they contain more bases; even the forest and farm soils are not rich in potassium and calcium (as is shown by comparison of all the Sese samples with the sample H from the mainland). The supply of available nutrients in sample G from a stretch of *Hyparrhenia diplandra* grassland is intermediate between that of *Loudetia* grassland and of forest soils, and therefore the existence of tree seedlings in the *Hyparrhenia* grassland can be explained on account of its superior fertility to *Loudetia* grassland, for *Hyparrhenia diplandra* is a much more vigorous species than *Loudetia kagerensis*, and therefore root competition cannot be the controlling factor. The poverty of bases is reflected in the acid nature of all the Sese soils (excluding those of

Phot. 1. View from Bugala Island southwards over Fumve Island. In the foreground ironstone outcrops surrounded with *Eragrostis blepharoglumis* then slopes of *Loudetia kagerensis* down to mixed lakeside forest.



Phot. 2. Bukasa Island. Lakeside forest on a rocky headland; the trees are *Uapaca guineensis*, *Piptadenia Buchananii* and *Ficus Drewei* Hutch.

Phot. 3. Bugala Island. Forest in which *Piptadenia Buchananii* is dominant, intermixed with *Maesopsis Eminii*; the grass beside the path is *Eragrostis blepharoglumis.*

Phot. 4. Bugala Island. An old anthill colony near the lakeside forest. A ring of *Harungana madagascarensis* around a group of *Maesopsis Eminii.*

Phot. 5. Bugala Island. Upper forest edge. Scrub of *Smithia Kotschyi*, *Pteridium aquilinum*, etc.; to the left *Raphia monbuttorum*, behind it *Conopharyngia Holstii*: to the right the large leaves of *Anthocleista Schweinfurthii* and behind it *Maesopsis Eminii*.

Phot. 6. Bugala Island. Abandoned farm. Clumps of *Musa sapientum* and *Saccharum officinarum* still remain, but most of the ground is colonized by scrub in which *Leonotis nepetaefolia* is prominent.

Buninga), and the many samples which have been examined have reactions lying between *p*H 4·0 and 5·5. As a rule the grassland soils are richer in organic matter than are forest soils, owing to the mass of grass roots, although most of the dead leaves are consumed by termites whose covered runs form a network over the surface; most of the leaves and twigs that fall in the forests are destroyed on the surface by fungi, bacteria and termites and do not become incorporated in the soil; the unexpectedly small amount of organic matter in the soil is characteristic of most tropical forests (Vageler, 1933). It may also be noted that the depth of the forest and farm soils is less than that of the grassland soils; the layer of ironstone near the surface of patches of good soil has not stunted the growth of plants but has been beneficial in preventing percolation of the soil solution and the loss of nutrients. In many places trees grow so well on sheets of ironstone almost bare of soil that it seems there may be a slow reversal of the process of laterization and that the concretions may break down under the influence of moisture and warmth, or of the plant roots, liberating a supply of nutrients.

Table 1

Locality	Depth cm.	Nature	Available nutrients %		
			P_2O_5	K_2O	CaO
A. Bugala. Lakeside forest, *Uapaca guineensis* dominant	0– 10	Dark sandy	0·0076	0·022	Nil
	10– 60	Dark grey sandy	0·0043	0·005	Nil
	60– 75	,,	0·0021	0·009	Nil
B. Bugala. Base of slope of grassland, near site A, *Loudetia kagerensis* dominant	0– 28	Grey sand	0·0053	0·007	Trace
	28– 52	Darker grey sand	0·0016	0·005	,,
	52–120	Light grey sand	0·0016	0·007	,,
C. Bugala. Top of slope of grassland. *Loudetia kagerensis* dominant (concretionary layer at 90 cm.)	0– 15	—	0·0107	0·0085	0·008
	15– 30		0·0114	0·0044	0·006
	30– 60	—	0·0107	0·0021	0·008
	60– 90	– –	0·0103	0·0270	0·085
D. Bugala. Upper forest near site C (concretionary layer at 30 cm.)	0– 5	Root mat	0·0072	0·047	0·058
	5– 20	Sandy	0·0081	0·021	0·011
	20– 50	,,	0·0077	0·015	0·005
	50– 80	Heavier and stickier	0·0084	0·012	—
E. Bugala. Good farm with healthy bananas (ironstone at 40 cm.)	0– 15	Black	0·0118	0·057	0·508
	15– 38	Water standing at 38 cm.	0·0118	0·027	0·140
F. Bugala. Poor farm with unhealthy coffee (ironstone at 50 cm.)	0– 15	Red sandy loam	0·0096	0·012	0·031
	15– 30	,,	0·0112	0·013	0·030
	30– 50	,,	0·0072	0·006	0·017
G. Bukasa. Grassland. *Hyparrhenia diplandra* dominant	0– 15	Red	0·0118	0·0147	Trace
	15– 25	,,	0·0081	0·0136	,,
	25– 48	,,	0·0100	0·0161	,,
	48– 75	Brown subsoil	0·0103	0·0131	,,
	75–120	,,	—	-	-
H. Mainland, elephant grass zone (Bukalasa)	0– 22	-	0·0078	0·093	0·538

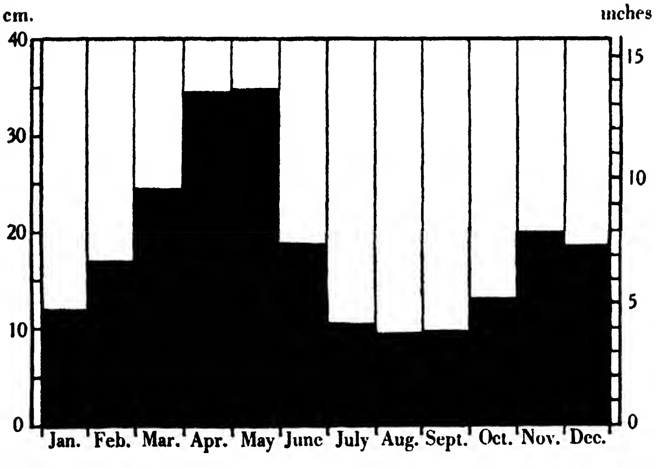
The suggestion that the bases are the limiting factors of soil fertility is supported by comparison of samples E and F, from good and bad patches on a Bugala farm. The soil of the good area is more shallow than that of the poor area, but the content of bases is much higher (owing to the lack of percolation) and appears to be the factor controlling fertility. On account of the soil poverty, in the few instances where dressings of kraal manure have been applied to the farms there has been a striking response in the vigour of the bananas and the coffee trees. It is noteworthy on the Sese Islands that when plots of coffee have been planted partly in the open and partly in the shade of large spreading trees, the shaded coffee always is in much better health—the leaves are dark green and good crops are borne—than the unshaded, whose leaves are yellow and which bear little fruit after they are 2 or 3 years old. Shade has an important effect in increasing the rate of photosynthesis of coffee (Nutman, 1937), while the supply of potassium has great influence on the process of assimilation in all plants; it is highly probable that the poor condition of coffee in the open on the Sese Islands is due to the combination of lack of shade and of a deficiency in potash. No significant differences were found in the nitrate content of shaded and unshaded soil on Sese; the amounts of nitrate in tropical soils appear to alter rapidly according to climatic conditions, but as a general rule in Uganda the nitrate content of shaded soil is less than that of unshaded, and the difference between unshaded and shaded coffee therefore cannot be attributed to this factor.

About 70 miles to the south of the Sese Islands on the western shore of Lake Victoria lies the Bukoba district of Tanganyika. The climate and scenery of the north of Bukoba resembles that of Sese, or rather of the islands as they must have been when they were densely populated, for in Bukoba all the better land is occupied by farms. In between the farms lie wide belts of short grassland in which *Loudetia kagerensis* is dominant, while *Maesopsis Eminii* and *Harungana madagascarensis* are two of the most typical woody species, as in the Sese Islands. Milne (1938) has described the pedology of Bukoba and its influence on agriculture and has shown that the soils there, like those of Sese, have been derived from rocks poor in plant nutrients and have been further impoverished by leaching; in Bukoba also there often occurs the layer of concretionary ironstone near the tops of the hills. Milne has shown that the soils of the Bukoba grasslands, though rich in organic matter which has been claimed to be the major factor in soil fertility, and fairly well supplied with phosphates, yet are very acid and are deficient in the bases which support plant life. There is a dense population in Bukoba, but in spite of the pressure on land, Milne has pointed out that the area of the farms cannot be increased on account of the poverty of the grasslands. Cultivations sometimes are made in grassland, but the Bambara groundnut, *Voandzeia subterranea* Thou., and the 'Numbu' yam, *Coleus dysentericus* Bak., are the only crops that can be grown; after they have been harvested, months elapse before the ground is colonized by ephemeral weeds and 8 or 9 years must pass before nutrients sufficient to produce another crop have accumulated.

THE CLIMATE OF THE SESE ISLANDS

The average annual rainfall of the Sese Islands amounts to over 2 m. and is very well distributed; the distribution of tropical rainfall may have a more important bearing on plant growth than does the total precipitation; the intensity of the dry season is the important factor, for water supply may be a limiting factor only in such periods (Thomas, 1933). The average precipitation per month at Kalangala on Bugala Island for the years 1924–37 is shown in the diagram:

	mm.
January	120
February	168
March	244
April	346
May	347
June	189
July	107
August	96
September	97
October	129
November	200
December	184
	2227



Monthly average precipitation in the Sese Islands over a period of thirteen years

This rainfall is of the equatorial type, with two wet seasons, the main one in March, April, May and a lesser one in November and December; but rain may be expected every month. Heavy storms occur; in 1938 the heaviest rainfall in 24 hr. was 72 mm.—but much of the rainfall is in small showers; in 1938, 2830 mm. fell on 142 days. Dry spells may be expected in January and during July, August and September, but it is seldom that the grassland becomes dry enough to burn vigorously. The only complete records of temperature on the Sese Islands are those given by Hale Carpenter (1920); he showed that the average temperature for each month of the year was about 22° C., and did not fluctuate more than 1° C. above or below that figure, while the average daily range was small. The relative humidity of air also showed little fluctuation, and the averages lay between 72 and 77 %. The combination of heavy well-distributed rainfall and equable temperature might be expected to produce the evergreen growth and abundance of epiphytes found in the Sese forests; the short sparse grasslands seem foreign to this zone, and factors other than climate must be responsible for their presence.

Discussion

The main factors controlling the distribution of plants are soil, climate and the influence of man and stock. The last factor in a country like Uganda, which has been populated for many centuries, has completely altered the vegetation over much of the countryside; apart from the swamps, the higher zones of some of the mountains and the relatively small areas of virgin forest, none of the plant associations can be regarded as climaxes, all have been caused, and are still being altered, by the actions of man and of stock.

It is highly probable that the Sese Islands originally were completely covered with forest, and that when the forests were cleared for cultivation much of the inherently infertile soil soon became more impoverished and the farms were concentrated on the patches of better soil; this process has been discussed by Milne (1938) in the case of Bukoba. The Sese grassland is not a primary grassland, nor in fact do many of the Uganda grasslands seem to be primary with the exception of those high on the mountains: once the forest has been destroyed, the balance of the chemical and biological soil process is upset as described by Milne in Trinidad (1940) and Lebrun in the Belgian Congo (1938), and the soil becomes too impoverished to support the growth of trees. The very wet warm climate near the lake appears to have been quite as important as the nature of the parent rocks in producing the poor soils of the Sese Islands, for similar vegetation patches of forest and stretches of *Loudetia kagerensis* grassland, and similar poor soils and sheets of ironstone, are characteristic of the headlands on the shore of Lake Victoria, only 30 miles north of the Sese Islands. These headlands are derived from rocks of the Basement Complex, and the same rocks a few miles inland have given rise to richer soils on which elephant grass, *Pennisetum purpureum*, becomes dominant.

Michelmore (1939) has brought forward the theory that seasonal flooding or waterlogging is the prime cause of the formation of open grasslands in tropical Africa. Michelmore admits that this theory must be modified in the case of Uganda. Numerous examples can be quoted to show that in the west of Uganda the reverse of his theory is the case, the forests are on the waterlogged soils and the grassland is on the drier slopes of the hills. The vegetation of the Sese Islands is an instance; the forest is concentrated by the lake shore near the seepage level and on the flat tops of the hills, where percolation is prevented by the sheets of ironstone and which are swampy for long periods in the rainy seasons. Michelmore also suggests that physical or chemical soil differences, apart from waterlogging, are of little importance in determining the presence or absence of trees, but that richer soils may favour the presence of open grassland. This statement also is quite contrary to the general experience in Uganda; wherever open grassland and closed forest are contiguous, the grassland soils are poorer than those of the forests, on account of the degradation caused by clearing. In other parts of the tropics also the persistence of open grasslands, such as the savannahs of British Guiana, appears to be connected with a poor supply of plant nutrients.

In addition to the effect of clearing, cultivation and burning have a great influence on the soil and vegetation; while stock, by their grazing, treading and manuring action may greatly alter the herbage. When the islands were densely populated, large numbers of cattle were kept and their influence was important. But during the time when the islands were evacuated neither grazing (except for the relatively small areas browsed by sititunga and hippopotami) nor burning (except for the fires started occasionally by lightning) were of any importance; the moist equable climate favoured the growth of evergreen forest with an abundance of epiphytes, such as covered the farmlands, yet forest growth could encroach only very slowly on to the grassland, and it is obvious that soil poverty was the inhibiting factor. There is much evidence to support this view: the manner in which tree growth starts at the water seepage level and around anthills, places where an accumulation of plant nutrients would be expected; the scarcity of grasses such as *Cynodon* spp. and *Brachiaria* spp. which denote high soil fertility; and the predominance of ferns both in the undergrowth of forests and in the scrub at the forest edge. Bracken, *Pteridium aquilinum,* is one of the most widespread higher plants in the world; it is the sole representative of the British flora which is common in all parts of the tropics—and in Uganda as in other places it is an indicator of poor acid soil. In fact, the predominance of all pteridophytes may be regarded as an indication of poor soil, as shown by Wardlaw (1931) to be the case on the abandoned banana lands of St Lucia. On the Sese Islands more ferns have been found (forty species are recorded) than in any other part of Uganda, and they form a more important constituent of the vegetation than in any other localities with the exception of some of the mountain forests. In studies of tropical plant ecology, the most stress is always laid upon the influence of climate; climate is responsible for the distinction between the main zones of vegetation, but it is seldom realized how much edaphic factors are responsible for local differences in plant communities.

The relation between forest and grassland is not static, however, for the trees are encroaching slowly on the grassland, and if the population of the islands reverted to the former density, the process would be reversed. In the case of the Sese Islands the term climax would be used only in two extremes when the vegetation would be in equilibrium with its environment. The first instance would be the case when the population is so dense that all the land is under grassland or farms, as in Bukoba to-day: Milne (1938) has pointed out that the area of farmland cannot be extended unless fertilizers are imported to the district. The second instance would be that of the original state of the islands when they were under a complete forest cover; it is impossible to guess how long it would take for the vegetation to revert to this state, for while *Uapaca* might remain as the dominant tree in some swampy hollows, yet there is little doubt that the soft-wooded quick-growing species now abundant would be replaced by others typical of 'virgin' forest.

Not only may the influence of soil factors determine the composition of the wild vegetation, but it has an even more important bearing on the problems of agriculture; in the case of the Sese Islands and of Bukoba, development is controlled by the supply of plant nutrients, and the studies embodied in this paper, which were commenced in an attempt to throw light on the problems of coffee cultivation in Sese, have shown that soil poverty is the most important factor. Our knowledge of the interaction of factors controlling the growth and fruiting of tropical crops is very incomplete: all too often it has been stated that a crop requires so much rainfall per annum, regardless of the distribution, and 'forest soil', regardless of the fact that some forests have rich and some have poor soils. Irreparable damage has been done when forests have been cleared and large plantations made in districts where the soil is inherently poor—a good example being the history of the plantations in the Usambara Mountains in Tanganyika (Milne, 1937). Many of the statements of crop requirements that have been made in the past must be modified: for example, in areas of west Uganda where coffee has had a short productive life, tea has proved to be a very profitable crop in spite of the fact that the soils are not sufficiently acid and the rainfall is too sparse to conform with the requirements of the pundits. More careful analysis of the climatic and edaphic factors is needed, for empirical rules that apply in one country will not do so in another, and the differences between the response of each tropical crop to various manures show that the plants have different requirements of nutrients and are best suited to different soils.

The relationship between soil types and the composition of the vegetation has not been studied in the tropics to the same extent as in temperate regions; some correlations have been established, for example, in India (Hole & Singh, 1916) and in British Guiana (Davis & Richards, 1939), but Northern Rhodesia is the only territory of East Africa where these ecological studies have been carried out on a large scale (Trapnell, 1937). There Trapnell utilized associations of woody plants to classify the country into vegetation and soil units. In Uganda the natural woodlands have been so much cut and burnt by man that in many places only vestiges of the original vegetation now remain, and it seems that the grasses are the most valuable group of indicator plants (Thomas, 1940); this hypothesis is in agreement with experience in the United States of America where, as Sampson (1939) has pointed out, at present grazing indicators are the best understood and most successfully used.

The supply of nutrients and the influence of man and stock appear to be of greater importance than the climate in controlling the distribution of grass species in Uganda, and numerous examples from the vegetation of the Sese Islands can be quoted in support of this hypothesis. On the one hand, there is the scarcity in Sese of many grasses, such as *Cynodon* spp., *Brachiaria* spp. and *Pennisetum purpureum*, that are abundant on the richer soils of the mainland close to the islands, growing under climatic conditions similar to those of Sese. On the other hand, many of the grasses that are abundant on the islands are found on poor sandy soils in parts where the climatic conditions are very different from those of Sese. *Loudetia kagerensis* is dominant on patches of grassland in the Ankole district, where the rainfall is unevenly distributed and amounts to less than half that of the Sese Islands, but where the soils are derived from rocks of the same Karagwe Ankolean system as on the islands. *Eragrostis blepharoglumis*, which is dominant around outcrops of quartzite on the Sese Islands, is also dominant on similar outcrops in the Kigezi district at altitude up to 2100 m., where the temperatures are very much lower. *Pennisetum polystachyon* Schult., a species which is locally dominant near some of the pits dug on the Sese grassland for smoking fish, growing on the excavated sandy soil, is very uncommon on the mainland near the islands, but it is the dominant grass on poor sandy abandoned farmlands of the Lango district, 200 miles to the north, where the vegetation is dry savannah forest. It is interesting to note that in some genera, for example *Loudetia* and *Eragrostis*, which comprise the bulk of the grasses on the Sese Islands, all the species in Uganda are indicative of poor soil; while in other genera, for example *Pennisetum*, some species like *P. polystachyon* are excluded by other grasses from any but the poorest soils and others like *P. purpureum*, elephant grass, and *P. clandestinum* Hochst., Kikuyu grass, only become dominant on rich soils.

Grasses seem destined to play an increasingly important part in tropical agriculture. The immemorial practice of shifting cultivation, whereby exhausted farmlands were allowed to revert to grassland or bush, was much condemned until a few years ago and it was considered that tropical land might be kept continuously under cultivation if green manure crops were included in the rotation. But it is now becoming evident that grass leys furnish the most feasible method of maintaining and restoring soil fertility in many parts of the tropics. Most of the species which are useful for grass leys require special conditions of soil and treatment and usually the grasses of most value for grazing will not grow on poor soils. Experiments at Nyakato in Bukoba have shown that heavy dressings of fertilizers must be given if the *Loudetia kagerensis* in the grassland is to be replaced by more nutritious species. Not only may the study of natural grasslands afford valuable information concerning the soils but also it furnishes a cheaper and quicker means of discovering the requirements of grasses in cultivation than would be given by experimental planting. For the same reason, studies of tropical crops in the wild state are of great value in solving the problems connected with the growth of these crops in cultivation; for example, observations on the wild populations of coffee in the Uganda forests have thrown much light on the questions of culture and of breeding. Ecological studies are of vital importance to tropical agriculture and their economic worth is slowly gaining recognition.

SUMMARY

1. The vegetation of the Sese Islands, a small group in Lake Victoria, is described; the islands are remarkable on account of the sharp division between belts of tropical evergreen forest and short sparse grassland.

2. Particulars are given of the climate and of the soils; on account of the heavy well-distributed rainfall and the equable temperature it would be expected that the islands would be covered with forest. When the islands were evacuated of men and stock for over ten years the farms quickly reverted to secondary forest, yet the trees spread very slowly into the grassland.

3. Analyses have shown that none of the Sese soils are rich in plant nutrients, but that when samples in close proximity are taken from the grassland and from the forest, the supply of bases in the forest soils is greater than that in the grassland soils which contain a very small proportion of available plant nutrients; the differences in composition of the soil are the factors controlling the distribution of vegetation.

4. The influence of soil poverty on the agriculture of Sese and of Bukoba (where similar conditions obtain) is discussed and it is suggested that insufficient importance has been attached to edaphic factors in tropical ecology, especially in its relation to agricultural problems.

Grateful acknowledgement is paid to the Director and Staff of the Herbarium at the Royal Botanic Gardens, Kew, for the determinations of plants collected; to Dr Griffith and Dr Martin of the Uganda Department of Agriculture and to the East African Meteorological Service for rainfall records.

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REVIEW

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 10, No. 1, May 1941

This number, starting the tenth year of the *Journal*, contains eight papers, two reviews, 144 Notices of Publications on Animal Ecology of the British Isles, and a summary of the Society's business. The fact that most of the notices refer to papers published in 1940 illustrates the vitality of natural history and biology in this country under wartime conditions. The papers deal with ecological survey, census methods, population dynamics, food ecology and environmental optima and range. J. R. Erichsen Jones's quantitative survey of the fauna of the River Dovey in West Wales provides a normal standard, from an unpolluted river, for comparing previous surveys in lead and zinc polluted rivers. There were about 132 species, but this comparative richness was probably due more to the favourable placidity of the lower levels than to the absence of metallic pollution. K. Radway Allen's elaborate discussion of the food habits of young salmon in Rivers Eden and Thurso, relates the stomach analysis to previous quantitative survey results. He obtains interesting figures illustrating the degree of availability of different food species, and the amount of selection exercised by the fish. On the whole, the fish food was representative of the total fauna, with certain distortions caused by availability. A rather similar idea about availability (in this case, to the human observer) is contained in two papers on bird census methods: M. K. Colquhoun and Averil Morley's study of downland bird densities. Both papers give general accounts of the bird populations, but special attention is paid to the influence of the relative conspicuousness of different species on the population counts obtained.

H. F. Barnes continues and summarizes his 14 years' population analysis of wheat blossom midges and their parasites, showing fluctuations and the relation of these to wheat yield under different conditions. H. N. Southern and J. S. Watson describe the food contents of 40 fox stomachs, and some other records of fox food. Although there was a great range of food (including insects) the common one was rabbits, both on the Welsh hills and the English plains. E. Emrys Watkins gives an account of seasonal changes in populations of *Corophium volutator*, an Amphipod Crustacean living in soil at the margins of brackish water in the River Dovey; also the relative habitat distribution of this and *C. arenarium*. The first species was proved to turn over its population through two generations each year. Gwendolen Rees gives a very complete account of the environmental limits of a marine flatworm, *Monocelis fusca*, living in a small marine rock pool at Aberystwyth. The temperature and salinity tolerance ranges were determined both in the field and by experiment.

Reviews deal with the *Journal of Ecology* and with marking experiments on rodents and butterflies.

Charles Elton

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BRITISH ECOLOGICAL SOCIETY

BIOLOGICAL FLORA OF THE BRITISH ISLES

FOREWORD

AT the Annual Meeting of the British Ecological Society at Oxford in January 1940 it was decided to take up again the publication of a British Biological Flora, which had already been projected in 1928 (A Proposed Biological Flora of Britain, E. J. Salisbury, *J. Ecol.* **16**, 161). The Council of the Society have now made arrangements for the publication of such a Flora. They feel that in the ordinary ecological experience of members of the Society there has been accumulated much information about the biology and ecology of individual species of British plants, and that this information, if collected, would make a very valuable body of reference. There is also much scattered published information which could be made more readily accessible in the new Flora.

The Council therefore invite all members of the Society to an active co-operation in gathering together this material, and they would welcome also assistance from all botanists and field naturalists who, although not members of the Society, may be willing to help. Assistance can be given either by sending information to the authors who have accounts in preparation, or by offering, singly or in collaboration, to prepare accounts of species themselves. It is felt that the present wartime circumstances, which are unfavourable to long-term investigation and to much field work, may not be so unfavourable to the sorting out of data which have, for the most part, already been collected. It is quite understood that these accounts will not be in any sense final or complete, and no one should be deterred from offering assistance from a feeling that his own knowledge is too scanty.

The Flora will take the form of accounts of single species or small groups of species, by various authors. These accounts will not be published in any regular order, but species will be dealt with as the necessary information becomes available. The account of each species will be as far as possible self-contained, but short general accounts of at least the larger genera will be included, and in these, to avoid repetition, information applicable to all the species will be given.

The accounts will appear in the first instance in the *Journal of Ecology*. They will then be reissued and sold separately as they appear. It will be possible to place a standing order for them.

It is hoped that the Flora will eventually become a complete account of the biology of all British Flowering Plants, Conifers, and Pteridophytes, including naturalized aliens. In order not to delay publication indefinitely accounts will be published even if the information is incomplete in many particulars. The accounts will thus be summaries of the information at present available about each species, rather than miniature monographs. In general outline the accounts of each species will be based on the Schedule for Contributors printed after this foreword. The method of treatment may, however, have to be varied in particular instances, either because some species demand somewhat different treatment, or because of the nature of the existing information. For some species, too, there may be valuable and relevant data, e.g. genetical, cytological, physiological, or biochemical, of a kind not yet available for others. Such data will be incorporated even though not falling clearly under any of the headings of the schedule. A brief diagnosis of the species, mentioning ecological as well as morphological distinctions from other British species of the genus, will precede each account, and each species will be numbered as in the *London Catalogue of British Plants*, Ed. XI (1925). References to published work will be in the standard form adopted in the Journal; and acknowledgments of unpublished information should be made by enclosing in brackets the name of the authority with no following date (e.g. (Cruttwell)).

The publication of the Flora will be in the control of the Council of the Society, but initiation of the publication and the preparation of the first instalments have been left in the hands of the Hon. Editor of the *Journal of Ecology*, Dr A. R. Clapham and Dr P. W. Richards. They will constitute a committee which will invite authors to prepare accounts of particular species. Those who accept such invitations will be asked to co-operate with the committee and to attend those meetings of the committee at which the publication and organisation of work connected with their own accounts are dealt with.

The Council attaches great importance to the accuracy of identification of animals mentioned in the Flora, and to the use of reliable authorities for statements about animals. To ensure this the committee will have the assistance of Dr O. W. Richards. The scheme for the treatment of these references will be found in a note at the end of the Schedule. Similar assistance with the references to the Fungi has been kindly promised by Dr Alex. Smith. Communications about the Flora should be addressed to:

Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield, 10;
or Dr A. R. Clapham, University Department of Botany, Oxford;
or Dr P. W. Richards, Botany School, Cambridge;
or Dr H. Godwin (Hon. Sec.), Botany School, Cambridge.

BRITISH ECOLOGICAL SOCIETY

BIOLOGICAL FLORA OF THE BRITISH ISLES

SCHEDULE FOR CONTRIBUTORS

I. (*a*) General distribution and abundance of the species in the district or districts described.

   (*b*) Altitudinal limits.

   (*c*) Other topographical limitations, e.g. restriction to north- or south-facing slopes, to open or shaded habitats, etc.

II. (1) Brief general description of the habitat or habitats.

   (2) Description of the substratum.

   Where a species occupies a great variety of habitats it may be impossible to give precise information under the following headings, but some indication of ranges and of the characteristics of the most frequent habitats will be valuable.

   (*a*) Parent material.
   (*b*) Appearance of the soil profile.
   (*c*) Height and seasonal variation of the water table.
   (*d*) Abundance of worms and other burrowing animals.
   (*e*) Rate of incorporation and decay of humus.
   (*f*) Appearance and texture of raw humus or peat, if present.
   (*g*) *p*H at different depths (state how determined). The depths should be selected in relation to the layers of the soil profile and the rooting depth of the characteristic plants.
   (*h*) Humus content or 'loss on ignition'.
   (*i*) $CaCO_3$ content.
   (*j*) Other chemical analyses (potassium, phosphate, total nitrogen, nitrate nitrogen, etc.).
   (*k*) Mechanical analyses.

   (3) Other features of the habitat, e.g.:

   (*a*) Light intensity and its seasonal variation in relation to the life history of the species in question.
   (*b*) Humidity of the air.
   (*c*) Exposure to wind.

III. Communities in which the species occurs, with its frequency in each and with lists of closely associated species.

   Complete lists with frequency symbols will be welcome, but lists only of the chief associated species and especially of the dominants will be adequate. It is important that any one list should refer only to one kind of habitat and to restricted areas, of about 1 sq. m., including the species in question. Lists should include characteristic species of other groups than Flowering Plants, if possible.

IV. Response of the species to biotic factors such as felling, burning, coppicing, mowing, peat-cutting, grazing, rabbit-nibbling, trampling, manuring, ploughing, etc.

V. (*a*) Gregariousness (solitary plants, large patches, small patches).
  (*b*) Performance of the plant in its various habitats, e.g. average height; whether flowering freely, poorly or not at all.
  (*c*) Sensitiveness to frost, drought and other exceptional weather conditions.

VI. (*a*) Morphology of underground parts.
  (*b*) Depth, direction of growth and length of underground stem and functional roots.
  (*c*) Presence or absence of mycorrhiza.
  (*d*) Mode of perennation and general description of winter conditions.
  (*e*) Mode and rate of vegetative reproduction and spread.
  (*f*) Longevity of the individual plant.
  (*g*) Age of plant at first flowering.
  (*h*) Does the plant set seed (or produce seedlings) every year or at what intervals?
  (*i*) Are any ecotypes known or suspected?
  (*j*) Chromosome number, with authority.

VII. (*a*) Times of maximum growth of roots and other underground organs.
  (*b*) Time of appearance of new leafy shoots.
  (*c*) Time of flowering.
  (*d*) Time of maturation and shedding of seeds.
  (*e*) Time and place of germination of seeds.

VIII. (*a*) Mode of pollination of flowers.
  (*b*) Insect visitors to flowers and their behaviour.
  (*c*) Are cleistogamic flowers produced and, if so, when?
  (*d*) Is reproduction amphi- or apo-mictic?
  (*e*) Does vivipary occur?
  (*f*) Does the species hybridize? By what criteria are the hybrids recognized as such? To what extent do the hybrids show a diminished fertility as compared with the parents? Do they show any differences in ecological behaviour?
  (*g*) Average numbers of seeds per fruit and per plant.
  (*h*) Mode of seed dispersal and special features, if any, e.g. seeds tend to stick together.
  (*i*) Viability of seeds (state how determined).
  (*j*) Special conditions affecting germination, e.g. sensitivity to light, necessity for preliminary freezing, etc.
  (*k*) Short description and sketch of young seedlings.
  (*l*) Relative importance of reproduction by seed and by vegetative means.

IX. (*a*) Insects feeding on the plant and the part or parts eaten by them.
(*b*) Plant parasites.
(*c*) Serious diseases. Describe the symptoms and give the names of the causal organisms, if any. Assess as far as possible the importance of the damage done by the diseases. Does the incidence of the disease vary with habitat and season?

X. History of the species as a member of the British flora, with notes on fossil records, dates of introduction of denizens and aliens, etc.

NOTE ON REFERENCES TO INSECTS (O. W. RICHARDS)

The lists of insects will in general be restricted to those closely associated with a single genus or species of plant, but may include some which feed on two or more allied genera of plants, or on a few genera living in the same habitat. Insects for which the records do not state the individual species of plants will be listed only in the accounts of genera.

Sometimes insects with polyphagous feeding habits may actually be more common on a plant than the restricted feeders, but the list of general feeders would be extremely long and very difficult to make complete. Where a general feeder is actually known to be a serious check to a plant, the record will be included.

Only British insects will be listed, but they will include some whose feeding habits may have been observed only on the Continent. Records will be given of the British distribution, in a very condensed form, where there is reason to think the information reliable. Absence of records often means that an insect has not been collected rather than that it is not present. The very imperfect state of the records of insect feeding habits and distribution must be stressed.

Lists will be given of the larger works from which records have been taken, and of the experts who have been consulted.

BRITISH ECOLOGICAL SOCIETY

BIOLOGICAL FLORA OF THE BRITISH ISLES

ACCOUNTS PUBLISHED OR IN PREPARATION

The accounts already published are:

Juncus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. inflexus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. effusus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. conglomeratus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. subnodulosus Schrank., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

The following are being prepared:

Andromeda polifolia L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield, 10.
Juncus squarrosus L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield, 10.
Rhamnus catharticus L., Dr H. Godwin, Botany School, Cambridge.
Frangula alnus Mill., Dr H. Godwin, Botany School, Cambridge.
Juncus macer Gray (*J. tenuis* Willd.), Dr P. W. Richards, Botany School, Cambridge.
J. filiformis L., Dr P. W. Richards, Botany School, Cambridge.
Tilia cordata Mill., H. A. Hyde, National Museum of Wales, Cardiff.
T. platyphyllos Scop., H. A. Hyde, National Museum of Wales, Cardiff.
Aconitum anglicum Stapf., H. A. Hyde, National Museum of Wales, Cardiff.
Scilla non-scripta (L.) Hoffm. and Link, G. E. Blackman, Imperial College of Science, London, S.W. 7.
Juncus articulatus L., Dr A. R. Clapham, University Department of Botany, High St., Oxford.
J. sylvaticus Reich., Dr A. R. Clapham, University Department of Botany, High St., Oxford.
Asperula odorata L., Dr A. R. Clapham. University Department of Botany, High St., Oxford.
Cladium Mariscus Br., Dr V. M. Conway, Department of Botany, The University, Sheffield, 10.
Acer Pseudoplatanus L., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
Zostera L. , T. G. Tutin, Department of Botany, The University, Manchester.
Myosotis arvensis (L.) Hill, A. E. Wade, National Museum of Wales, Cardiff.
M. versicolor Sm. (*M. lutea* (Cav.) Pers.), A. E. Wade, National Museum of Wales, Cardiff.
M. collina Hoffm., A. E. Wade, National Museum of Wales, Cardiff.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account, singly or in collaboration, should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

JUNCUS L.

P. W. Richards and A. R. Clapham

There are 25 or 26 British species, which are grouped in the following sections:

1. Poiophylli. Flowering stem usually with cauline leaves, seldom scapose. Leaves generally flat or channelled, rarely cylindrical or laterally compressed. Flowers with prophylls. *J. squarrosus*, *J. macer*, *J. Dudleyi*, *J. compressus*, *J. Gerardii*, *J. trifidus*, *J. bufonius.*

2. Genuini. Flowering stem scapose, with sheathing scale leaves at the base, prolonged by a bract so that the inflorescence appears lateral. *J. inflexus*, *J. effusus*, *J. conglomeratus*, *J. filiformis*, *J. balticus.*

3. Thalassii. Flowering stem scapose, bearing at the base leaves with a green cylindrical lamina. Inflorescence appearing more or less lateral. *J. maritimus*, *J. acutus.*

4. Graminifolii. Flowering stem scapose or leafy. Inflorescence capitate. Flowers without prophylls. *J. capitatus.*

5. Septati. Flowering stem generally leafy. Leaves cylindrical or laterally compressed, hollow with obvious transverse septa. *J. subnodulosus*, *J. sylvaticus*, *J. articulatus*, *J. alpinus*, *J. Marshallii*, *J. bulbosus*, *J. Kochii* (=*J. bulbosus* var. *Kochii*), *J. pygmaeus.*

6. Alpini. Flowering stem generally leafy at the base. Leaves cylindrical to filiform, indistinctly septate. Inflorescence terminal, of one to a few heads, each few-flowered. *J. castaneus*, *J. biglumis*, *J. triglumis.*

The species, except for *J. compressus*, *J. Gerardii* and *J. articulatus* and its allies, keep distinct from each other and are readily separated.

Habit. All the species are herbaceous with a characteristic ('rush-like') habit. The development of the underground stem varies from a very short root-stock (e.g. *J. squarrosus*) to an extensively creeping rhizome (e.g. *J. sylvaticus*). In many species, especially among the Genuini, the rhizome has numerous short branches radiating from a centre and the internodes are short, so that the plant forms dense tufts; in such species the tufts tend to die away in the middle, so that "fairy rings" may be formed.

Roots, mycorrhiza. The roots are often dimorphic, some straight, unbranched and descending, others branched and ascending. They have persistent root-hairs and are said to have no mycorrhiza.

Leaves. The leaves vary greatly in morphological detail but are always long and relatively narrow.

Flowers. The flowers have an inconspicuous perianth, are wind-pollinated, protogynous and, in many species, open in 'pulses'. "For some days, perhaps, no flowers will open; then suddenly, without apparently any change in the weather to account for it, the flowers will all open together" (Avebury).

The flowering season usually begins after, or very little before, midsummer. No species are known to be apomictic. *J. bufonius* is commonly, and other species occasionally, cleistogamous. Hybrids are generally sterile and are infrequent, except in the Septati. The seeds are small and light and either mucilaginous or dry; dispersal is by wind, by animals and cart wheels (in the species with mucilaginous seeds) or possibly by water.

Seedlings. The seeds of most species germinate in spring. Early stages in germination are very similar in four species examined: *J. effusus*, *conglomeratus*, *inflexus* (Genuini) and *J. subnodulosus* (Septati). The base of the cotyledon emerges first, curving down towards the soil and becoming attached by a circlet of root-hairs. Early growth is most rapid in the middle region of the cotyledon, which erects and straightens except for an apical hook from which the seed is suspended. The very young seedling is whitish, becoming green only when the cotyledon has become hooked. The hypocotyl remains very short and the radicle emerges from the swollen basal disk, just below the circlet of hairs. All four species bear leaves with green laminae in the seedling stage.

Life-form. *J. bufonius*, *J. capitatus* and *J. pygmaeus* are therophytes: all three of these species, it may be noted, belong to different sections of the genus. The majority are hemicryptophytes, rosette (*J. squarrosus*); semi-rosette without running branches (*J. effusus*); or semi-rosette with running branches (*J. bulbosus*); some are rhizome geophytes (*J. maritimus*) or helophytes (*J. subnodulosus*). The distinction between the species which are hemicryptophytes, geophytes and helophytes is not sharp; in some species the life-form varies; thus *J. bulbosus* can be a hemicryptophyte, a helophyte or even a hydrophyte.

Ecology. All the British species grow in habitats either permanently or periodically wet, and are for the most part intolerant of shade. They exhibit a wide range in base requirement, some being markedly eutrophic (*J. subnodulosus*, *J. inflexus*) or even halophilous (*J. maritimus*, *J. acutus*, *J. Gerardii*), while others are calcifuge (*J. squarrosus*, *J. bulbosus*). None is extremely oligotrophic.

Morphology of tufted and creeping types

The morphology of *J. inflexus* and *J. subnodulosus* may be described as representative, respectively, of the tufted and far-creeping species of *Juncus*.

A tuft of *J. inflexus* consists of a sympodial system of radiating branched rhizomes from which arise crowded erect aerial shoots, almost in contact at the base but spreading upwards in a brush-like manner. Aerial shoots are of two kinds: (i) flowering shoots bearing an apparently lateral inflorescence; and (ii) sterile shoots. Both terminate very short segments of the sympodial rhizome, there being usually six scale leaves in all; a prophyll, a scale subtending the continuation-bud and four scales on the erect portion. The basal scale of the four (the third on the sympodial segment) subtends a bud which becomes a lateral branch of the rhizome. The remaining three have no axillary buds. Each scale is a glossy dark brown sheath, sometimes with a short terminal awn, but never with a well-developed lamina. Above the scales an uppermost leaf, the bract, whose sheath encloses the young terminal inflorescence, has a well-developed erect cylindrical green lamina which appears to continue the stem upwards. The long internode between the uppermost leaf and the scales is green and is the main assimilating region of the flowering shoots. The sterile shoots bear a leaf resembling the bract (often erroneously referred to as a sterile stem), but much longer and with no internodal extension below it. The abortive growing point of the short sterile shoot is enclosed by the very inconspicuous sheath of this stem-like leaf.

The rhizome grows horizontally and is freely branched from the axils of the basal scales of the erect shoots, buds being borne alternately to right and to left of the main rhizome. Most of the branches become 'spurs' of very limited growth, sympodial like the main rhizome, but bearing only 1–6 erect shoots; but others become 'long shoots' of unlimited growth. Since internodal elongation is very slight and branches arise from the bases of almost all erect shoots, the rhizome system is condensed and the plant is tufted, not far-creeping like *J. sylvaticus* or *J. subnodulosus.* On the other hand, the spurs being very short, vegetative spread is most rapid along the radially directed long shoots, and the tufts are less compact than in *J. effusus* and *J. conglomeratus.* The rhizome runs horizontally at a depth of 1½–3 in. below the surface.

Numerous adventitious roots are borne on the rhizome. The majority grow almost vertically downwards to 6–9 in. (15–22·5 cm.) below the surface. Some arise in autumn and some in early spring (April), and they function for one season only. They are at first pale yellow, quite unbranched and covered throughout with persistent root-hairs. Some bear a few branches near the base, but these arise late. While still functional these roots are stout and straight, but they persist after death for many years, becoming dark red and slightly flexuous. In this condition they are easily compressed, in contrast with the firm functional roots. Besides these vertically growing roots there are also a few roots arising from the sides and top of the main rhizome, and especially from spurs, which grow towards the soil surface and branch freely.

Of other caespitose species, *J. conglomeratus* and *J. effusus* resemble *J. inflexus* very closely in their morphology. *J. acutus* and *J. maritimus* differ in bearing the continuation-bud of the rhizome in the axil of the fourth instead of the second scale; in that many of the basal leaves have laminae and in that the much shorter bract does not appear as an upward prolongation of the stem. *J. biglumis* and *J. triglumis* are also caespitose in habit, but have true leaves. *J. squarrosus*, with a different and less regular mode of growth, will be described in detail in the account of that species.

J. subnodulosus is a far-creeping plant with rhizomes often reaching many feet in length and, where the plant is dominant, becoming densely intertwined in a mat-like growth about 2–3 in. (5–8 cm.) below the surface. The rhizome is sympodial, as in *J. inflexus*, each segment bearing two scale-leaves at a distance of ½–1 in. before erecting to become an aerial shoot. The renewal-bud is in the axil of the second scale, and a bud which gives rise to a lateral branch of the rhizome, usually of limited growth, is in the axil of the third scale, at the base of the erect part of the segment. Lateral branches or 'spurs' are borne alternately left and right of the main sympodium. They are sympodial, like the parent axis, but with much shorter intermodes, so that their erect shoots are closely crowded, only about a quarter of an inch apart. They arise in small groups of 2–6 at the bases of adjacent erect shoots, separated by lengths of rhizomes with no spurs. The erect shoots are of two kinds, as in *J. inflexus*: (i) flowering shoots with 3–5 basal scales consisting of sheaths with no lamina or only a short awl-like point and usually two foliage leaves with sheaths and long cylindrical laminae; and (ii) sterile shoots with basal scales and long, cylindrical stem-like leaf. The root-system is dimorphic, of stout, straight unbranched roots growing vertically downwards and slender much-branched roots directed sideways or upwards.

Of other creeping species, *J. sylvaticus* resembles *J. subnodulosus* very closely in its morphology, but lacks the monophyllous sterile shoots, while *J. bulbosus* and *J. Kochii* differ further in having a more slender rhizome-system and in a tendency to form epigeal stolons. *J. balticus*, of section Genuini, lacks foliage leaves, but is otherwise similar to *J. subnodulosus*, while *J. filiformis*, of the same section, creeps in some substrata but not in others. Some species of the section Poiophylli also creep, but do not constantly bear the continuation-bud of the rhizome in the axil of the second scale. Thus, in *J. trifidus*, the axillant scale is the second or fourth, and in *J. compressus*, the second, fourth or sixth.

Among the Septati, *J. articulatus* and its close allies are often subcaespitose and emphasize the general morphological similarity of the rhizome in caespitose and creeping types. There is no essential difference in mode of branching, but the distinction between long and short shoots is greatest in the far-creeping types and least in such densely tufted types as *J. effusus*; and short shoots may be borne at the base of all the erect shoots of the main rhizome in tufted types, but only at intervals in far-creeping types. The root-system may be dimorphic in both types.

INSECTS AND FUNGI ASSOCIATED WITH *JUNCUS*

INSECTS (O. W. RICHARDS)

The following is a fairly complete list of British *Juncus* feeders. Only species very closely associated with *Juncus* are included, not more or less polyphagous species. The species have all been observed in Great Britain, but the feeding habits may have been recorded only on the Continent. Records are given of the British distribution, in a very condensed form, where there is reason to think the information is reliable. Where no host names are given, the records do not state the species of *Juncus*.

HEMIPTERA-HOMOPTERA.

PSYLLIDAE: *Livia juncorum* Latr.; galls on flowers, c.; *Juncus inflexus*, *J. effusus*, *J. conglomeratus*, *J. bulbosus*, *J. articulatus*, *J. sylvaticus*. *Psylla bagnalli* Harr. Northumberland, Ebudes.

DELPHACIDAE: *Conomelus limbatus* (Fab.); sucks and oviposits in stems, c., England, Scotland; *Juncus conglomeratus*, *J. effusus*, probably *Juncus* spp. *Conomelus lepidus* (Boh.); c., England. *Delphacodes douglasi* (Scott.), *D. reyi* (Fieb.); suck stems.

JASSIDAE: *Macrosteles horvathi* Wagner; sucks stems.

HEMIPTERA-HETEROPTERA.

TINGITIDAE: *Serenthia laeta* Fall.; local, southern England to Lancs.

CAPSIDAE: *Teratocoris saundersi* D. & S.; local, British Isles. *Poeciloscytus palustris* Reut.; Hants, Carmarthen. *Cyrtorrhinus caricis* (Fall.); British Isles, c. *C. pygmaeus* (Zett.); England, c. *C. flaveolus* (Reut.); southern England, local; probably eating eggs of *Conomelus*, etc.

COLEOPTERA.

BUPRESTIDAE: *Aphanisticus emarginatus* (Oliv.); swept from rushes in Isle of Wight (bred from mines in stem of *Juncus* spp. on Continent).

DIPTERA.

CECIDOMYIDAE: *Lestodiplosis liviae* Rübs.; inquiline in gall of *Livia*, Durham (Bagnall and Harrison, 1924).

AGROMYZIDAE: *Dizygomyza luctuosa* (Meig.); adult flies recorded commonly from Britain (on Continent mines *Juncus effusus* and probably other spp.).

HYMENOPTERA.

TENTHREDINIDAE: *Eutomostethus luteiventris* (Klug.); c., mines as young larvae, external feeder on various Gramineae later. *Dolerus anticus* Klug; England, very local (bred in Holland from *Juncus effusus*). *Dolerus madidus* Klug (bred in Germany from *Juncus conglomeratus*) and *Dolerus triplicatus* Klug; c., England; external feeders. *Selandria serva* (Fab.); England, c., and *S. sixii* Vollenh.; England, local. Both external feeders on *Juncus*, *Carex* and Gramineae.

LEPIDOPTERA.

NOCTUIDAE: *Coenobia rufa* (Haw.); England to Cheshire, Ireland, local; mines stems of *Juncus articulatus*.

TORTRICIDAE: *Bactra lanceolana* (Hb.); British Isles, v.c.; mines stems of

Juncus, *Scirpus*, *Cyperus*. *Bactra furfurana* (Haw.); British Isles, local; mines stems of *Juncus conglomeratus* and *Eleocharis palustris*.

GLYPHIPTERYGIDAE: *Glyphipteryx thrasonella* (Scop.); British Isles, v.c.; mines stems.

ELACHISTIDAE: *Elachista scirpi* Staint.; S. England to Norfolk and Pembroke, local; mines leaves of *Juncus compressus* and *Scirpus maritimus*.

COLEOPHORIDAE: eat seeds: *Coleophora caespititiella* Zell.; British Isles, v.c.; frequent on *Juncus effusus*, *conglomeratus*, *Gerardii*, *squarrosus*, less frequent on *J. articulatus* and *inflexus*. *Coleophora glaucicolella* Wood; S. England to Hereford and Cambs., c.; frequent on *Juncus inflexus*, less frequent on *J. effusus*, *conglomeratus*, *Gerardii*, *articulatus*. *Coleophora agrammella* Wood; S. England to Hereford and Essex, local; *Juncus effusus*, *conglomeratus*, *articulatus*. *Coleophora adjunctella* Hodgk.; S. England to Lancs, local; *Juncus Gerardii*, *compressus*. *Coleophora galactaula* Meyr.; S. England to Hereford and Cambs., local; *Juncus articulatus*. *Coleophora obtusella* Staint.; Kent to Devon and Lincoln, local; *Juncus maritimus*.

A list is given below of the larger works from which records have been taken. Very valuable information and advice have also been supplied by the following gentlemen: W. E. China (Brit. Mus., Hemiptera), R. B. Benson (Brit. Mus., Hymenoptera), G. D. Morison (Marischal College, Aberdeen, Thysanoptera), H. F. Barnes (Rothamsted Experimental Station, Diptera, Cecidomyidae).

Butler, E. A. (**1923**) *A Biology of the British Hemiptera-Heteroptera*. London.

Davidson, J. (**1925**). *A List of British Aphides*. London.

Edwards, J. (**1896**). *The Hemiptera-Homoptera of the British Islands*. London.

Fowler, W. W. (**1887–1913**). *The Coleoptera of the British Islands*. 6 vols. London.

Haupt, H. (**1935**). In *Die Tierwelt Mitteleuropas*, **4**, Lief. 3, Zikaden. Leipzig.

Hendel, F. (**1927**). In Lindner's *Die Fliegen der Paläarktischen Region*, **49**, Lief. 16–19, Trypetidae. Stuttgart.

Hendel, F. (**1931–6**). In Lindner's *Die Fliegen der Palaarktischen Region*, **59**, Lief. 52, 54, 56, 58, 66, 85, 90, 92, 94, 96. Agromyzidae. Stuttgart.

Hering, M. (**1935–7**). *Die Blatt-Minen Mittel- und Nord-Europas*. 6. Lief. Neubrandenburg.

Houard, C. (**1908–13**). *Les Zoocécidies des plantes d'Europe et du Bassin de la Méditerranée*. 3 vols. Paris.

Meyrick, E. (**1928**). *A Revised Handbook of the British Lepidoptera*. London.

Theobald, F. V. (**1926–9**) *The Plant Lice or Aphididae of Great Britain*. 3 vols. London.

FUNGI

Buchenau (1906) states that in spite of their high tannin content the Juncaceae are rapidly destroyed by endophytic fungi, and that 220 species of fungi have been recorded from members of the family. Nevertheless, there are comparatively few British records on *Juncus* spp., and most are of saprophytes on dead stems and leaves. The only rust recorded is *Uromyces Junci* (Desm.) Tul. on *Juncus subnodulosus*, with aecidial stages on *Pulicaria dysenterica*, and the only smuts *Entorrhiza Aschersoniana* (Magn.) de Toni, in roots of *Juncus* *bufonius*, and perhaps *Entorrhiza Casparyana* (Magn.) de Toni in roots of *Juncus squarrosus*. No other obligate parasites seem to have been recorded. The following saprophytes are known only from *Juncus*:

ASCOMYCETES.

DISCOMYCETES: *Dasyscypha conformis* (Cke.) Sacc., *D. diminuta* (Rob. & Desm.) Sacc., *D. stigmella* (Cke.) Sacc., *Gorgoniceps micrometra* (B. & Br.) Sacc., *Mollisia Curreyana* Phill., *Sclerotinia Curreyana* (Berk.) Karst., *Trichopeziza fugiens* (Phill.) Sacc., all on moribund or dead stems and leaves of several or unspecified *Juncus* spp.

PYRENOMYCETES: *Claviceps Junci* Adams; *Didymosphaeria enormis* Grove; *Hypocrea Placentula* (Grove) on *Juncus effusus*; *Leptosphaeria juncina* (Auersw.) Sacc. on *Juncus conglomeratus, effusus, articulatus*; *Leptosphaeria maritima* (C. & Plow.) Sacc. on *Juncus maritimus*; *Phyllachora Junci* (Fr.) Fckl.; *Pleospora juncigena* Cke., *Pl. Junci* Pass. & Beltr.; *Phomatospora therophila* (Desm.) Sacc. All on moribund or dead stems and leaves.

FUNGI IMPERFECTI

COELOMYCETES: *Discula Junci* Sm. & Ramsb. on dead culms of *Juncus communis* which contain *Sclerotium roseum*; *Hendersonia juncina* J. W. Ellis on *Juncus effusus* (and *J. acutus* in Channel Islands); *Leptostroma Juncacearum* Sacc. on *Juncus conglomeratus, ? effusus, maritimus*; *Leptostromella juncina* Sacc. on *Juncus articulatus, conglomeratus, effusus, inflexus*; *Microdiplodia Junci* Died. on *Juncus maritimus*; *Phoma neglecta* Desm. on *Juncus effusus, maritimus*; *Placosphaeria Junci* Bubak on *Juncus effusus, conglomeratus*; *Pycnothyrium junci* Grove on *Juncus communis* sens. lat.; *Septoria Junci* Desm. on *Juncus effusus, conglomeratus, maritimus*; *Stagonospora bufonia* Bres. on *Juncus Gerardii*; *Stagonospora innumerosa* Sacc. on *Juncus effusus, maritimus*; *Stagonospora junciseda* Sacc.; *Stagonospora socia* Grove on *Juncus conglomeratus*; *Stagonospora trimera* Sacc. on *Juncus maritimus*. All on moribund or dead stems and leaves.

HYPHOMYCETES: *Geotrichum roseum* Grove.

BASIDIOMYCETES.

HYMENOMYCETES: *Flammula juncina* Sm.

MYXOMYCETES

PLASMODIOPHORACEAE: *Ligniera Junci* (Schwartz) Maire and Tison, in roots of *Juncus* spp.

The above list has been compiled from the following sources:

Bisby, G. R. & Mason, E. W. (1940). List of Pyrenomycetes recorded for Britain, *Trans. Brit. Mycol. Soc.* **24**, 127.

Grove, W. B. (1913). *The British Rust Fungi (Uredinales).* Cambridge.

Grove, W. B. (1935, 1937). *British Stem- and Leaf-Fungi (Coelomycetes)*, vol. **1** (1935) and vol. **2** (1937). Cambridge.

Oudemans, C. A. J. A. (1919–1924). *Enumeratio Systematica Fungorum.* The Hague.

Saccardo, P. A. (1882–1913). *Sylloge Fungorum.*

L.C. No. **1894**

Juncus inflexus L. (*Juncus glaucus* Ehrh.)

P. W. RICHARDS AND A. R. CLAPHAM

Sect. GENUINI. In large dense grey-green tufts. Stems slender, erect, rigid, glaucous, dull, with 12–18 prominent ridges. Pith interrupted. Basal scales glossy, blackish or dark reddish brown. Inflorescence of many ascending branches, usually lax. Stamens 6. Capsules dark chestnut brown, glossy, ovoid, acuminate, mucronate, equalling or slightly longer than the perianth. Seeds reddish brown.

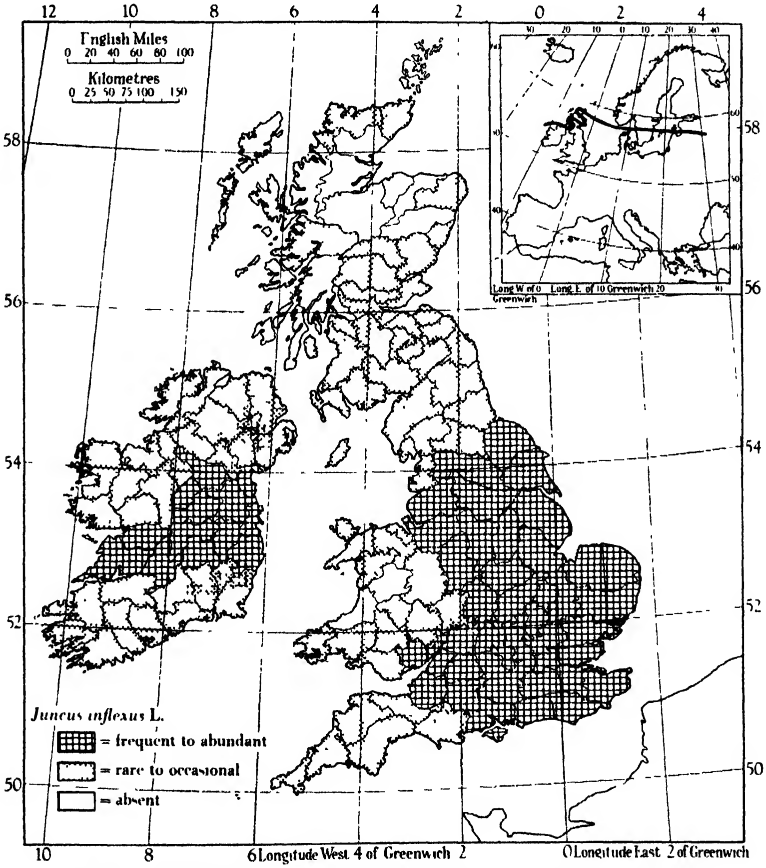

Fig. 1. *J. inflexus* L.: vice-comital distribution in the British Isles, and (inset) northern limit in Europe.

Not a very variable species. Markedly basicole, preferring stiff base-rich clays and alluvia (cf. *J. effusus*).

I. *Geographical and altitudinal distribution.* Present throughout most of Great Britain, abundant except in some northern and western counties and

Scottish Highlands. Not recorded for Cardigan (46), Montgomery (47), South Aberdeen (92), Banff (94), Moray (95), Easterness (97), Argyll (98), Dumbarton (99), Cantyre (101), South, Mid and North Ebudes (102–104), East and West Ross (105–106), South Sutherland (107), Outer Hebrides (110), Orkneys (111) and Shetlands (112). Present throughout Ireland.

Throughout Europe to Denmark, South Sweden, Latvia and Central Russia in the north and extending east to India and Mongolia; North Africa, Macaronesian Islands: introduced in South Africa and New Zealand.

Lowland, to 1450 ft. (442 m.) in Westmorland (Wilson, 1938), and 1500 ft. (457 m.) in Derbyshire (Baker, 1884). The higher records are all on calcareous rocks.

To 5741 ft. (1750 m.) in the Alps of Valais (Jaccard, quoted by Graebner, 1909) and to 5249 ft. (1600 m.) in Tyrol (Sarnthein, quoted by Graebner, 1909).

Usually in open situations; apparently intolerant of shade.

II. *Habitat.* In damp meadows, roadsides, openings in woods, etc., chiefly on heavy basic or neutral mineral soils, occasionally on fen peat, especially where consolidated by trampling. Often marginal to ponds on heavy basic soils. Normally absent on base-deficient soils, hence rare or absent in wide areas where acid soils predominate, e.g. Wales, Scotland. Conversely, in some calcareous districts, e.g. the immediate neighbourhood of Cambridge, almost completely replaces other Junci genuini. In parts of south, east and central England characteristically dominant in poorly drained undergrazed pastures on heavy basic clays or alluvium which may flood during winter but dries out in summer. Commonly found near springs and seepage lines where water is base-rich. Occurs in soils with more than 2 % NaCl (McCrea, 1926). Not found in habitats with water-table very close to or above surface throughout year. Profile in most of these habitats is a typical gleyed meadow soil. *p*H range in Lancashire and Yorkshire 6·5–7·7 (Pearsall: electrometric) and in Oxford district 5·9–7·8 (Cruttwell: colorimetric). Occurs in woods on suitable soils where illumination is good, e.g. rides, clearings, etc.

III. *Communities.* Most commonly a constituent of Agrostidetum stoloniferae which retains its essential floristic identity when *Juncus inflexus* is co-dominant with *Agrostis*, or even dominant. The following list is typical, species in brackets being most prominent when grazing is light:

Juncus inflexus	o.–d.	Agrostis alba var. stolonifera	a.–d.
(Festuca pratensis	f.)	Festuca rubra	l.
Holcus lanatus	l.a.	Dactylis glomerata	l.
Phleum pratense	f.	Poa pratensis	a.
Lolium perenne	l.	(Angelica sylvestris	l.f.)
Ranunculus repens	a.	Cerastium vulgatum	o.
R. acris	f.	Trifolium pratense	o.
Centaurea nigra	f.	Galium palustre	l.
Potentilla anserina	l.f.	Pulicaria dysenterica	l.
(Mentha aquatica	l.f.)	(Lotus uliginosus	l.)

Deschampsia caespitosa	l.	(Lathyrus pratensis	o.)
Trifolium repens	a.	Lysimachia Nummularia	o.
Prunella vulgaris	f.	Carex hirta	l.
Scabiosa succisa	f.	Galium uliginosum	l.
(Cirsium palustre	o.)	(Scrophularia aquatica	l.)
(Filipendula Ulmaria	l.f.)	Hypnum cuspidatum	a.

Adamson (1912) gives lists including *Juncus inflexus* from the wetter parts of an oak wood on calcareous Boulder Clay at Gamlingay in Cambridgeshire. *Filipendula* and *Deschampsia caespitosa* were co-dominant; *Juncus inflexus* and *Juncus effusus* both l.a., as were *Rosa arvensis, Rubus caesius* and *Carex remota*; *Lychnis Flos-cuculi* was abundant.

Other prominent species were:

Anemone nemorosa	o.	Calamagrostis lanceolata	o.
Viola Riviniana	o.	Epilobium hirsutum	o.
Fragaria vesca	o.–a.	Orchis mascula	o.
Nepeta Glechoma	o.	Arctium nemorosum	o.
Ficaria verna	o.	Pimpinella magna	o.
Viola sylvestris	o.	Carex vulpina	o.
Potentilla fragariastrum	o.	Lotus uliginosus	o.
Ajuga reptans	o.	Epilobium parviflorum	o.
Rumex viridis	o.	Barbula fallax	a.
Agrostis spp.	l.	Fissidens taxifolius	o.
Arctium minus	o.	Mnium undulatum	a.
Carex riparia	o.	Pellia spp.	f.

This society was found in lighter shade than typical Filipenduletum.

IV. *Response to biotic factors.* Tolerates annual mowing and light grazing, but does not readily invade pastures heavily grazed by cattle. Rapidly invades undergrazed damp pastures on suitable soils, since disliked by cattle. Protects more palatable species, e.g. *Juncus articulatus* and *J. sylvaticus*, growing near and among its tussocks. Eaten by rabbits (Breckland) probably only when grazing pressure is high. Appears tolerant of moderate trampling.

V. (*a*) *Gregariousness.* Usually social, 'individual plants form large spreading tufts which increase slowly in diameter until they are a foot across at the base. At this size the centre of the tuft usually begins to die off, but the diameter of the tuft may continue to increase until an irregular ring-like growth is produced. This may eventually break up into a number of separate tufts' (Cruttwell). Even when the species is dominant, tufts rarely fuse to form extensive continuous stands, as characteristic of *J. subnodulosus* and *J. sylvaticus*.

(*b*) *Performance in various habitats.* No information.

(*c*) *Effect of frost, drought, etc.* In one experiment only two seedlings out of 49 survived exposure to −4° C. for about 12 hr. In the same experiment 27 out of 43 seedlings of *J. effusus* and 33 out of 49 of *J. subnodulosus* survived.

VI. (*a*), (*b*) *Morphology.* Tufted, from a compact, horizontal, sympodial rhizome system (see introductory notes on *Juncus*). Continuation-bud of the sympodium in axil of second scale-leaf, and four more scales at base of erect portion of shoot segment. Spurs at base of all erect shoots, usually short with only 1–6 segments, so that growth radially outwards is more rapid, and the tuft less compact, than in *J. effusus* and *J. conglomeratus* whose spurs are longer. Rhizome at 1½–3 in. (4–7·5 cm.) below surface. Sterile shoots with long, cylindrical stem-like leaf. Root-system adventitious from rhizome, dimorphic. Most roots straight, unbranched, descending to 6–9 in. (15–22·5 cm.) below surface, arising in autumn and spring and functional for one season only, but persisting after death for many years, changing from pale yellow to dark red and becoming compressible and flexuous. Other more slender roots grow upwards towards soil surface and branch freely.

(*c*) *Mycorrhiza.* No information.

(*d*) *Perennation.* Semi-rosette hemicryptophyte, the greater part of both sterile and flowering shoots persistent and green during winter. Renewal buds at tip of rhizome and at bases of erect shoots and thus in surface layers of soil.

(*e*) *Vegetative reproduction* (see under V).

(*f*) *Longevity.* No information.

(*g*) *Age at* 1*st flowering.* Probably never before second growing season.

(*h*) *Frequency of seed production.* Reported in some localities to fail to ripen its seeds in some seasons: "frequently does not ripen its seed; practically all plants around Wadhurst Lake (Sussex) in 1931 were in this state" (Wolley-Dod, 1937).

VII. *Phenology.* (*a*) New roots arise, some in autumn and some in late March and early April, in Oxford district.

(*b*) New shoots first appear in March and early April (Oxford district), up to 9 in. high on 2 April 1941.

(*c*) Flowers in June and July in south England (in bud 7 June 1933, Breckland), perhaps later in the north. As in many other species of *Juncus*, flowering has an irregular periodicity. Flowers open early in morning, remaining open until midday, or later.

(*d*) Seeds shed from July to September, or later.

(*e*) Seeds germinate in April and May. Self-sown seedlings observed only in gardens. The rapid colonization of neglected low-lying meadows is probably by seed.

VIII. (*a*) *Mode of pollination.* Wind-pollinated, protogynous, anthers open a few hours after stigmas ripen.

(*c*) *Cleistogamy.* Buchenau (1906) reports that in Germany open flowers may not be found for as long as a week at a time in cold and damp weather, and supposes that cleistogamy takes place.

(*d*) *Apomixis.* Almost certainly amphimictic.

(*e*) *Vivipary.* Not observed.

(*f*) *Hybrids.* With *J. effusus* frequently found with the parents. "*J. diffusus* Hoppe" commonest, intermediate between parents and highly, if not completely, sterile. Other forms found more rarely, closer to one or other parent;

these produce apparently viable seed in fair quantity. They are presumably back-crosses of the F_1 with parent species. Hybrids with *J. conglomeratus* also reported in Britain, but must be very rare. Other hybrids known. In all cases hybrid status inferred from morphological characters and sterility. Available evidence suggests that factors isolating *J. inflexus* from *J. effusus* and *J. conglomeratus* are both ecological and genetical. "*J. diffusus* Hoppe" occurs where parent species are found together. No other data of its ecological requirements known.

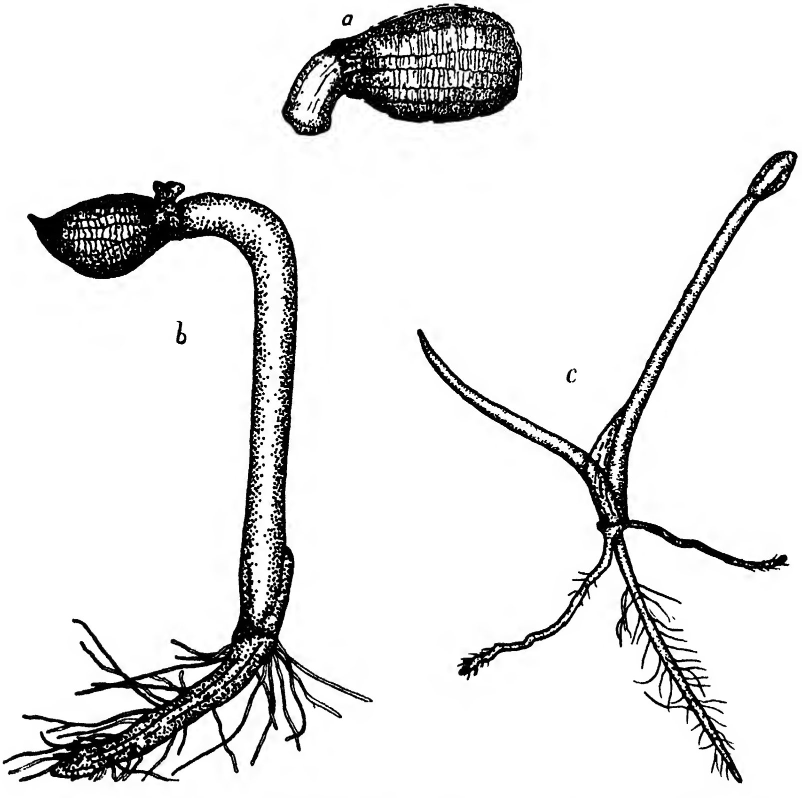

Fig. 2. Stages in germination of *Juncus inflexus*. Seeds from Cavenham Heath, W. Suffolk, sown in laboratory. (*a*) 13 days after sowing; ×37½. (*b*) 26 days after sowing; ×25. (*c*) 46 days after sowing; ×10.

(*g*) *Amount of seed.* Number of seeds per capsule variable, but usually about 100.

(*h*) *Dispersal.* Seeds dispersed by wind, probably also in mud by animals, wheels, etc., and perhaps by water; but when freed of their air-film they immediately sink. Seeds covered with film of mucilage, and become sticky when moistened. This often happens before they leave the capsule, so that they adhere together firmly.

(*i*) *Viability.* A proportion of shrivelled seed is non-viable, the remainder give a high percentage of germination (to 100 %). Viable for about seven years when stored dry.

(*j*) *Conditions for germination.* Seeds collected in autumn and sown in laboratory during following winter germinated only in light. If batches of seeds which have begun to germinate in light are transferred to dark, further germinations cease after the first day and are resumed only a few days (1–3) after returning to the light. Preliminary freezing of the seeds unnecessary. Germination probably "simultaneous" (cf. Salisbury, 1929).

(*k*) *Morphology of seedlings.* See introductory notes on *Juncus*, and Fig. 2. Seedlings have leaves with green laminae, as in other Junci genuini.

(*l*) *Relative importance of reproduction vegetatively and by seed.* No definite information available; probably both effective. Neglected meadows seem to be colonized by seed.

IX. *Parasites: diseases.* See introductory notes to *Juncus*. The Lepidopteran *Coleophora glaucicolella* Wood (Coleophoridae) is more common on *Juncus inflexus* than on other *Juncus* species.

X. *History.* No information.

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L.C. No. **1895**

Juncus effusus L. (*Juncus communis β effusus* E. Mey.)

P. W. Richards and A. R. Clapham

Sect. Genuini. Tall and stiffly erect in dense tufts. Stems soft, bright or yellowish green, glossy and smooth when quite fresh, with 40–90 fine striae. Pith continuous. Leaf-sheaths reddish brown, not glossy. Inflorescence about one-fifth from the apex of the apparent stem; many-flowered, lax or condensed into a rounded head. Sheath of lowest bract not inflated. Stamens 3. Capsules yellowish to chestnut brown, very glossy, broadly obovoid, retuse, not mucronate. Seeds yellowish.

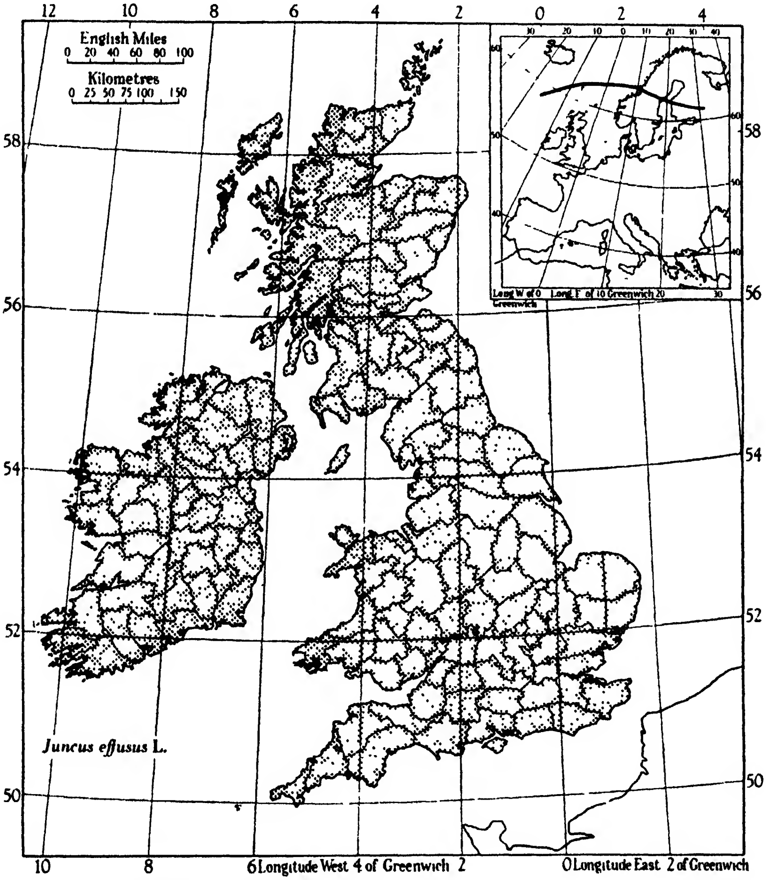

Fig. 1. *J. effusus* L.: present in all vice-counties of the British Isles. Inset map gives northern limit in Europe.

Varies greatly in the size of the whole plant and its parts, in colouring and in the compactness of the inflorescence. Ecologically it is the least exacting of the species of the genus as it is also the commonest and most widely distributed.

I. *Geographical and altitudinal distribution.* Present and abundant throughout the British Isles.

Throughout Europe to the Faeroes, to 64° 27′ N. in Norway and to 62° 45′ in Finland (Hermann, 1912); extending throughout the North Temperate Zone; less common in South Hemisphere.

Reaching 2000 ft. (610 m.) on Dartmoor (Martin & Fraser, 1939); 2400 ft. (732 m.) on Little Fell, Teesdale (Wilson, 1938); 2800 ft. (853 m.) in the Scottish Highlands (Druce, 1932), and in Co. Wicklow (Druce, 1932); 2050 ft. (623 m.) in Donegal (Hart, 1898). Often not extending as high as *Juncus conglomeratus*:

	J. effusus	*J. conglomeratus*	Authority
Moel Hebog	1100 ft. (335 m.)	1500 ft. (457 m.)	E. W. Jones
Berwyns	1200 ft. (366 m.)	1600 ft. (488 m.)	E. W. Jones
Breadalbane	1500 ft. (457 m.)	2750 ft. (838 m.)	White (1898)

In northern England (Pennines and Lake District) commonly found to 1600 ft. (488 m.) while *J. conglomeratus* is uncommon above 1000 ft. (305 m.). Extremes: *J. effusus* 2400 ft. (732 m.); *J. conglomeratus* 1900 ft. (580 m.). Both species occur at higher altitudes on soils overlying limestone or not extremely base-deficient.

Reaching 6888 ft. (2100 m.) in central Europe (cp. 6232 ft. (1900 m.) for *J. conglomeratus*). Thus *J. effusus* extends less far north than *J. conglomeratus* but locally may reach higher altitudes.

II. *Habitat.* Abundant and locally dominant in wet meadows, moors, woods and other damp habitats on a wide range of soils. Particularly characteristic of base-deficient mineral soils and of thin peat where the roots can reach mineral layers or non-calcareous flush water. Frequently abundant or dominant in communities marginal to ponds, lakes or streams in zone of fluctuating water-table. In undrained fens and bogs confined to marginal and streamside communities (e.g. laggs of raised bogs), but becoming abundant on drained or trampled peat. Not strictly calcifuge but much less common on basic soils and tolerant of high acidities. *p*H range in Oxford district at least 4·3–7·1 (Cruttwell), and in Pennines and Lake District 3·9–6·6. Appears to avoid substrata of extremely low base content; perhaps somewhat more exacting in this respect than *J. sylvaticus*. Probably confined to substrata aerated at least during part of the year, though somewhat less tolerant of drying out in summer than either *J. inflexus* or *J. conglomeratus*.

Usually in open situations but luxuriant in partial shade and frequent in damper parts of woods and in willow carr. Only *J. bulbosus* appears more tolerant of shade.

III. *Communities.* Associates include most of the common British plants of damp habitats. Very frequent associates are *Holcus lanatus*, *Agrostis alba*, *Scabiosa succisa, Cirsium palustre, Molinia coerulea* and *Polytrichum commune.* The following are representative lists:

(1) Juncetum effusi on stiff grey silt of the flood plain of the River Teifi between the big raised bogs at Tregaron near Aberystwyth: *Ranunculus acris, Cardamine pratensis, Galium palustre, Rumex acetosa, Carex acuta* and *C. Goodenowii, Molinia coerulea, Equisetum* sp. and *Sphagnum papillosum* (Godwin & Conway, 1939).

(2) In the 'lagg' at Tregaron *J. effusus* and the following are 'frequent to abundant': *Salix cinerea, Betula pubescens, Viola palustris, Lotus uliginosus, Comarum palustre, Hydrocotyle, Menyanthes, Scabiosa succisa, Carex Goodenowii, Holcus lanatus, Molinia coerulea* and *Sphagnum papillosum* (Godwin & Conway, 1939).

(3) Upland Junceta effusi (700–1900 ft. (213–580 m.)) in Wales, Dartmoor and the Pennines, usually have *Polytrichum commune* and *Sphagna* (especially *S. recurvum*) subdominant, and where the *Juncus* is dense there may be practically nothing else. This is a very widespread community in the west and north.

(4) A small alder-willow carr near Crickhowell, south Wales, had *Juncus effusus* locally dominant in partial shade with *Carex paniculata* l.d., *Juncus sylvaticus* v.a., *Hypnum cuspidatum* v.a., *Ranunculus repens* a. Also present were *Carex remota* and *C. sylvatica, Valeriana dioica, Ranunculus flammula, Galium palustre, Filipendula Ulmaria, Mentha aquatica, Lysimachia nemorum, Cirsium palustre, Rumex acetosa, Lotus uliginosus, Cardamine pratensis, Dryopteris spinulosa* and *D. dilatata, Mnium undulatum* and *Pellia epiphylla.*

IV. *Response to biotic factors.* More readily grazed by cattle and rabbits than *Juncus inflexus*, but not easily eliminated from neglected pastures merely by grazing. Readily invades undergrazed hill pastures, e.g. in Wales (cp. *J. inflexus* in undergrazed lowland pastures). Moderately resistant to trampling and tolerant of annual cutting for litter.

V. (*a*) *Gregariousness.* Grows in dense tufts which remain distinct, not forming continuous stands.

(*b*) *Performance in various habitats.* Most luxuriant in light shade and in small streams. Flowering less freely or not at all in heavier shade.

(*c*) *Effect of frost, drought, etc.* In one experiment 27 out of 43 seedlings survived exposure to −4° C. for about 12 hr.

VI. (*a*), (*b*) *Morphology.* Similar to *J. inflexus* (see introductory notes on *Juncus*) but even more densely caespitose and compact. Erect shoots more crowded, softer, taller and stouter than in *J. inflexus*, so that tufts appear denser. Spur-branches at bases of all erect shoots, longer than in *J. inflexus* and differing less from long shoots. Rhizome runs more or less horizontally at ¼–2 in. (0·6–5 cm.) below surface, forming a dense mat. Two kinds of roots. Most are stout and straight, penetrating vertically downwards into substratum to depth of 6–10 in. (15–25 cm.) below surface; also finer and much more freely branched roots extending sideways and upwards from rhizome.

(*c*) *Mycorrhiza.* No information.

(*d*) *Perennation.* Semi-rosette hemicryptophyte. Erect shoots tend to remain green during winter only in their lowest parts.

(*e*) *Vegetative reproduction.* By slow radial growth of the tufts.

(*f*) *Longevity.* No information.

(*g*) *Age at first flowering.* May sometimes flower in first season (more frequently than *J. conglomeratus* (Buchenau, 1906), but probably not before second year, in general.

(*h*) *Frequency of seed production.* Probably sets seed every year, but no definite information available.

(*i*) *Ecotypes.* No definite information but general observations suggest that form with condensed inflorescence (var. *congestus* Lej. & Court) prefers more acid conditions than species in general. The tall effuse form in woods, marshes and fens in south England is perhaps also ecologically distinct. Both these varieties may be ecotypes.

VII. (*a*), (*b*) *Phenology.* Roots and aerial shoots begin vigorous growth in March (Oxford district). *J. effusus* seems to be earlier than *J. inflexus.*

(*c*) Flowering early June to July in south England (buds and open flowers on 7 June 1933 in Breckland), and later in north (July–August). Irregularly periodic; perianth segments begin to open in evening and stigmas uncurl following morning on every second, third or rarely fourth day (Graebner, 1909).

(*d*) Fruiting in July and August (on 13 July 1933, in Breckland, all were in fruit); later in north. Seed shed over a long period after opening of the capsules (may still be collected in following April).

(*e*) Seedlings appear in April and early May in south England; mid-May to June in Pennines (Wattam, 1941). Usually seen on bare soil or mud or among *Sphagnum* (because not easily seen in closed vegetation?).

VIII. (*a*) *Mode of pollination.* By wind and occasionally by insects (Graebner, 1909). Flowers distinctly protogynous, stigmas uncurling a few hours before anthers dehisce. According to Graebner, self-pollination is frequent in Germany.

(*b*) *Pollinating insects.* No information.

(*c*) *Cleistogamy.* Occurs in Germany during unfavourable weather (Hansgirg, quoted by Graebner, 1909).

(*d*) *Apomixis.* Almost certainly amphimictic.

(*e*) *Vivipary.* Not seen.

(*f*) *Hybrids.* See under *J. inflexus* for "*J. diffusus* Hoppe". Hybrid with *J. conglomeratus*, with intermediate characters and high sterility, reported from Britain but needs confirmation. Infrequency of hybrids may be due to difference of flowering time (Buchenau, 1906), but the parents were in flower simultaneously at *c.* 1000 ft. in early July 1941 in South Wales.

(*g*) *Amount of seed.* No information.

(*h*) *Dispersal.* Seeds smaller, lighter and more mucilaginous than in *J.*

inflexus, showing stronger tendency to stick together. Dispersed partly by wind and partly by animals, especially after rain when seeds are sticky.

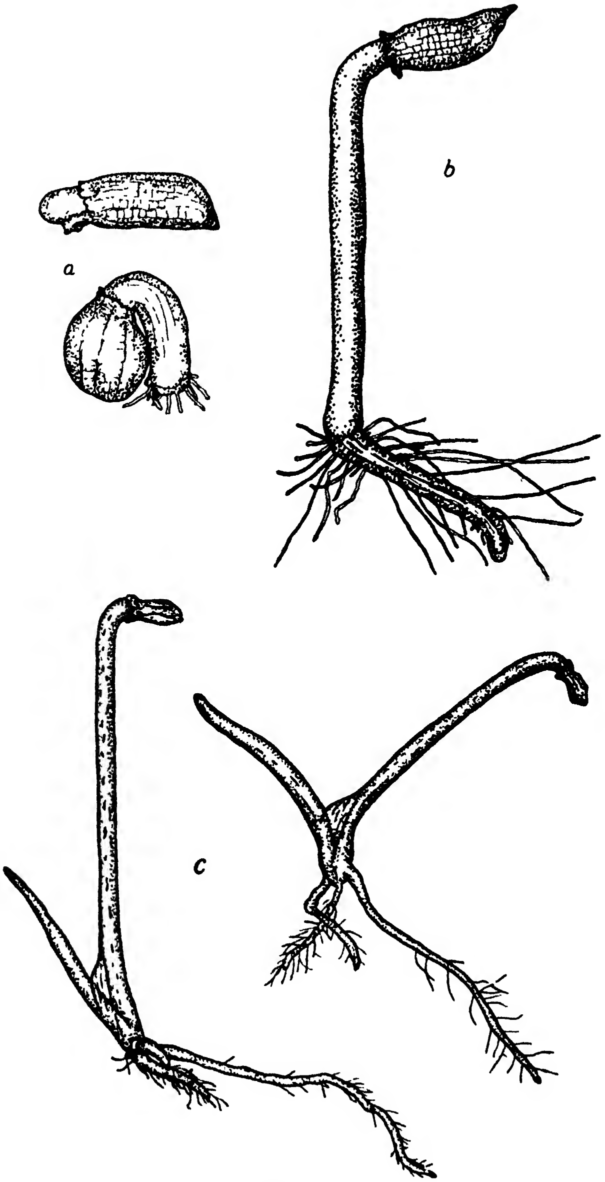

Fig. 2. Stages in germination of *Juncus effusus*. Seeds from Cavenham Heath, W. Suffolk, sown in laboratory. (*a*) 18 days after sowing; × 37½. (*b*) 26 days after sowing; × 37½. (*c*) 47 days after sowing; × 10.

(*i*) *Viability*. Smaller proportion of defective seeds than in *J. inflexus*. For Pennine material 97 % germination obtained in peaty soil (Wattam, 1941).

(*j*) *Conditions for germination.* Germination only in the light under laboratory conditions (see *J. inflexus*). Freezing unnecessary. Germination probably 'simultaneous' (Salisbury, 1929).

(*k*) *Morphology of seedlings.* See introductory notes on *Juncus*, and Fig. 2. As in other Junci genuini the seedlings have leaves with green laminae.

(*l*) *Effective reproduction.* No information, but probably both vegetatively and by seed. Vegetative reproduction seems the main agency in dense communities, with seedlings frequent around margins.

IX. *Parasites: diseases.* See introductory notes on *Juncus*. It is of interest that species of *Coleophora* (Lepidoptera-Coleophoridae) do not distinguish *Juncus effusus* and *J. conglomeratus*. Thus *Coleophora caespititiella* Zell., *C. glaucicolella* Wood and *C. agramella* Wood are found on both *Junci*.

X. *History.* No information.

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L.C. No. **1896**

Juncus conglomeratus L. (*J. communis* α *conglomeratus* E. Mey.; *J. Leersii* Marsson)

P. W. Richards and A. R. Clapham

Sect. Genuini. Closely resembling *Juncus effusus*, but usually less robust. Stem not glossy, with about 20 strong ridges especially prominent just below the inflorescence. Inflorescence usually reddish and condensed into a rounded head. Lowest bract with inflated sheath. Capsule as in *J. effusus* but usually with the remains of the style on a small elevation in the hollowed top.

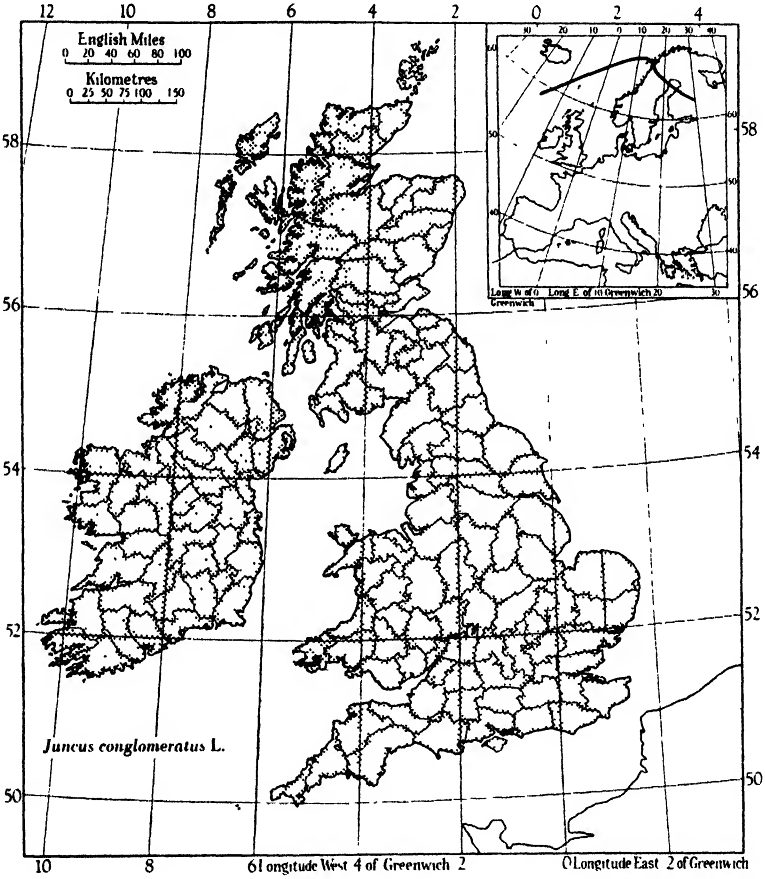

Fig. 1. *J. conglomeratus* L.: present in all vice-counties of the British Isles. Inset map gives northern limit in Europe.

Frequently confused with *J. effusus* and biologically very similar, but flowering earlier and having a somewhat smaller ecological range.

I. *Geographical and altitudinal distribution.* Reported from all Watsonian vice-counties of Great Britain and Ireland but in some the records need confirmation. Local or rare in many parts of south and east, abundant in north and west.

Throughout Europe extending north to Faeroes, to 68° 55′ in Norway, to 65° 50′ in Gulf of Bothnia, and across Russia to Siberia; north Africa, Asia Minor, Transcaucasia, Kurdistan; Newfoundland.

Reaching 2000 ft. (610 m.) on Dartmoor (Martin & Fraser, 1939); 1900 ft. (579 m.) in West Lancashire (Wheldon & Wilson, 1907); 1680 ft. (511 m.) in Lake District; 2570 ft. (783 m.) in the Carnedds, 2200 ft. (691 m.) on Arenig Fawr, 1740 ft. (530 m.) on Snowdon, 1600 ft. (488 m.) on the Berwyns and 1500 ft. (457 m.) on Moel Hebog (E. W. Jones); 1800 ft. (549 m.) in Black Mountains; 2750 ft. (838 m.) in Breadalbane and 2150 ft. (655 m.) in Atholl (White, 1898); 2250 ft. (686 m.) in Kerry (Druce, 1932); and 1700 ft. (518 m.) in Londonderry. Uncommon above 1000 ft. (305 m.) in Pennines and Lake District (Pearsall).

Reaching 5576 ft. (1700 m.) in the Alps of Valais (Jaccard, quoted by Graebner, 1909).

II. *Habitat.* In similar habitats to *J. effusus* and often associated with it, but more tolerant of dry conditions and perhaps less tolerant of flooding. Often on higher and drier ground marginal to flushes and slacks dominated by *J. effusus.* In Wales dominates parts (perhaps where grazing is heavy) of extensive Junceta on shallow peat over soft shales, especially below 1500 ft. (457 m.), e.g. on Silurian shales of central north Wales near Bala (E. W. Jones). Frequent at sides of roads and tracks.

On mineral soils and shallow peat or raw humus, less frequently on deep peat. In districts with predominantly basic soils, e.g. neighbourhoods of Oxford and Cambridge, uncommon, and almost confined to woods.

*p*H range in Pennines 5·09–6·82 (Pearsall; electrometric); near Oxford 5·5–7·1 (Cruttwell; colorimetric). On a gravelly heath near Reading, 4·6–4·9 (Pearsall). At 1450 ft. (442 m.) in central Wales on peat more than 10 in. (25 cm.) deep with *p*H 4·5 (colorimetric). Often stated to be more acidicole than *J. effusus*, but this impression may be given by its greater tolerance of dry conditions. Appears to be more basicole than *J. effusus* in Pennines (Pearsall).

III. *Communities.* Associated species much as for *J. effusus.* Thus at low levels in the Pennines (150–800 ft.) it is dominant or abundant with *Poa trivialis*, *Agrostis*, *Caltha* and *Ranunculus repens* in pasture; with *Glyceria fluitans* and *Alopecurus geniculatus* around a pond; with *Festuca* and *Poa* spp., *Dicranella squarrosa* and *Hypnum cuspidatum* in flush grassland; and with *Agrostis*, *Nardus* and *Hypnum cuspidatum* on thin trampled peat (Pearsall). Near Roughtor, Cornwall, it is very abundant with *Holcus lanatus* and *Festuca ovina* in a Molinietum with *Sphagna* locally dominant. Other abundant species are *Erica tetralix*, *Juncus squarrosus*, *Eriophorum angustifolium*, *Calluna*, *Narthecium*, *Juncus bulbosus*, *Viola palustris*, *Potentilla erecta*, *Luzula* *multiflora* var. *congesta*, *Aulacomnium palustre* (Magor, in Tansley, 1939). The upland Welsh Junceta conglomerati, like the more widespread Junceta effusi, have *Polytrichum commune* co-dominant or sub-dominant, in large cushions. 'In wetter examples, *Sphagna*, mainly *S. fallax*, *S. recurvum* and *S. amblyphyllum*, may also be co-dominant, while in drier examples there may be less *Polytrichum* but *Agrostis* and mosses such as *Hylocomium splendens*, *Hypnum Schreberi*, and *Hylocomium squarrosum* occur. This community is often exceedingly poor in species and may have practically nothing but *Juncus* and the mosses' (E. W. Jones). Above Pont-dol-goch, central Wales, besides *Polytrichum commune* and *Sphagna*, *Festuca ovina*, *Nardus*, *Molinia* and *Juncus squarrosus* are associated with sparsely dominant *J. conglomeratus*. In woods its associates are much as for *J. effusus*.

In Denmark, often with *Molinia* and *Nardus* (Wiinstedt, 1937).

IV. *Response to biotic factors.* As for *Juncus effusus*, but perhaps less heavily grazed and more resistant to trampling.

V. (*a*) *Gregariousness.* In habit very like *J. effusus* but tends to form smaller and less dense tufts. In Denmark, old tufts may become annular by death of the centre (Raunkiaer, quoted by Wiinstedt, 1937).

(*b*) *Performance in various habitats.* No information.

(*c*) *Effect of frost, drought, etc.* No information.

VI. *Morphology, etc.* As for *J. effusus*. Buchenau (1906) states that plants flower more rarely in the first season than *J. effusus*. No ecotypes known or suspected.

VII. (*a*), (*b*) *Phenology.* As for *J. effusus*, in the Oxford district.

(*c*) Begins to flower in May about a month earlier than *J. effusus*. In 1941 both species were in flower in early July at 1000–1500 ft. (305–457 m.) in south Wales; *J. conglomeratus* being distinctly more advanced.

(*d*) Fruits ripen July–September.

(*e*) Seeds germinate in April and May. Seedlings are usually seen on bare muddy ground, e.g. cart-ruts and mud churned up by cattle, etc. (E. W. Jones). This may be because it is difficult to observe them in closed vegetation.

VIII. (*a*) *Mode of pollination.* Wind-pollinated. Pollination by insects may take place occasionally, and self-pollination has been recorded in Denmark (Raunkiaer, quoted by Wiinstedt, 1937). More information is needed on these points.

(*b*) *Pollinating insects.* No information.

(*c*) *Cleistogamy.* Not recorded.

(*d*) *Apomixis.* Almost certainly amphimictic.

(*e*) *Vivipary.* Not recorded.

(*f*) *Hybrids.* See under *J. inflexus* and *J. effusus*.

(*g*) *Amount of seed.* No information.

(*h*) *Dispersal.* As for *J. effusus*.

(*i*) *Viability.* No information.

(*j*) *Conditions for germination.* No information.

(*k*) *Morphology of seedlings.* See introductory notes on *Juncus* and Fig. 2. Seedlings very like those of *J. effusus.*

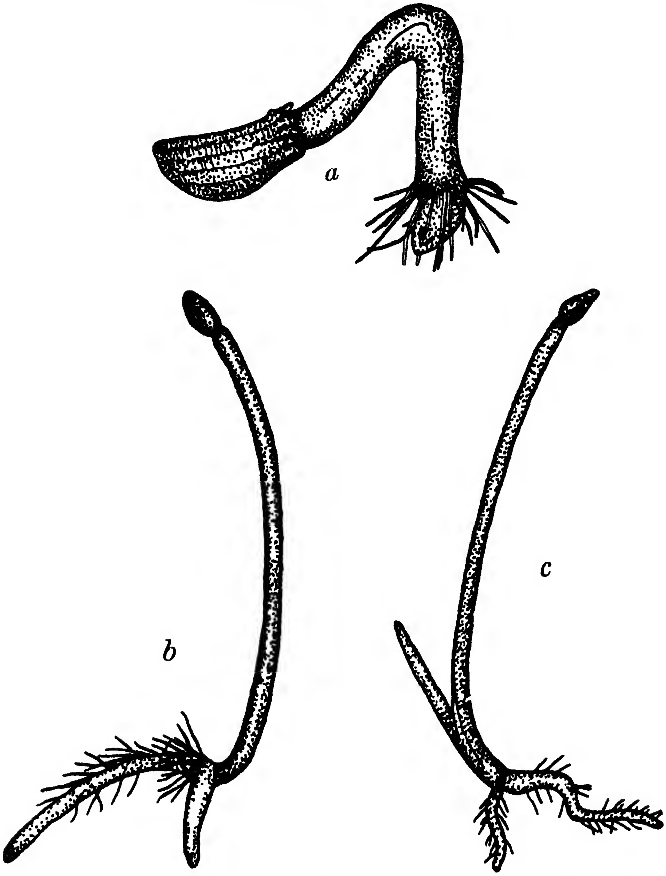

Fig. 2. Stages in germination of *Juncus conglomeratus*. Seed from Bagley Wood, nr. Oxford, sown in laboratory. (*a*) 8 days after sowing; × 40. (*b*) 15 days after sowing; × 10. (*c*) 20 days after sowing; × 10.

(*l*) *Effective reproduction.* Both vegetative and by seed. Sernander, (quoted by Wiinstedt, 1937) states that in Sweden flowering stems may fall to the ground and the seeds germinate in situ.

IX. *Parasites: diseases.* See introductory notes on *Juncus.*

X. *History.* No information.

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L.C. No. **1900**

Juncus subnodulosus Schrank (*J. obtusiflorus* Ehrh.)

P. W. Richards and A. R. Clapham

Sect. Septati. Tall, erect and rather soft, with a far-creeping horizontal rhizome. Stem and leaves similar, terete, bright green with both longitudinal and transverse septa, the latter at different levels, giving a step-like appearance when seen in longitudinal section. Flowering stems with brown basal scales and 1–2 long straight foliage leaves with 35–60 septa (contrast *J. sylvaticus* with only 18–25 septa). Sterile stems monophyllous. Inflorescence pale, repeatedly compound, of many heads of 3–12 or more flowers, the branches of the second order diverging at an angle of over 90°. Perianth segments obtuse

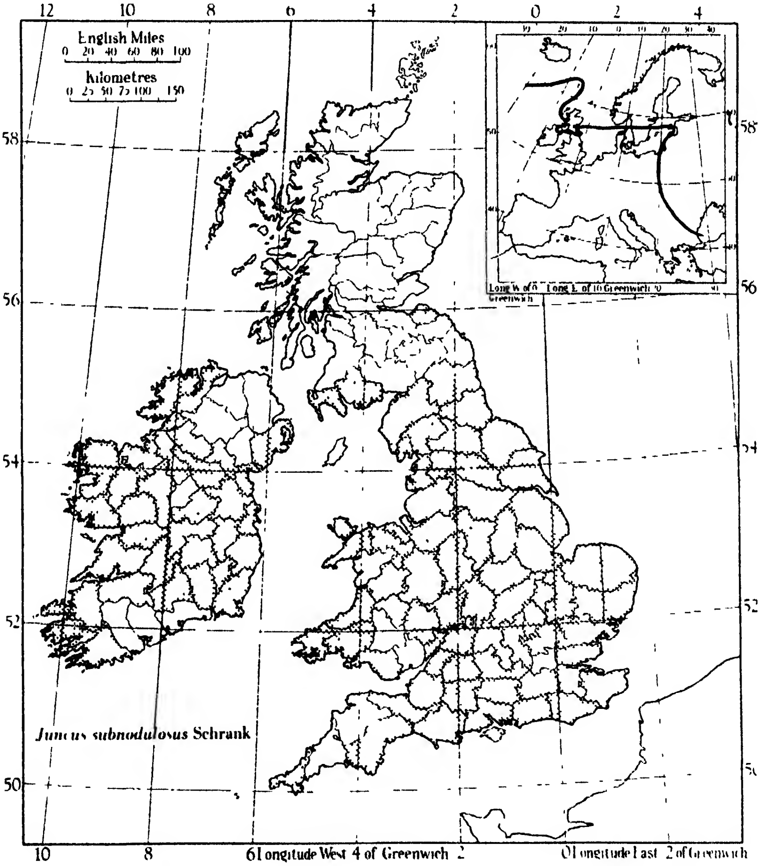

Fig. 1. *J. subnodulosus* Schrank: vice-comital distribution in the British Isles, and (inset) northern and eastern limit in Europe.

incurved, equal. Capsule slightly longer than the perianth segments, broadly ovoid, gradually tapering to a beak.

A very distinct species both morphologically and ecologically, varying little and having a narrow well-defined range of habitat, being almost restricted to calcareous peat.

I. *Geographical and altitudinal distribution.* Throughout England and Wales except East Cornwall (2), North Devon (4), Middlesex (21), Monmouth (35), Brecon (42), Merioneth (48), North Northumberland (68) and Westmorland (69). In Scotland found only in Wigtown (74), Kirkcudbright (73), East Lothian (82) and South Ebudes (102), so reaching only about 56° N. Absent from Isle of Man (71). In Ireland probably present everywhere except the north-east, being absent from Tyrone (36), Armagh (37), Antrim (39) and Londonderry (40).

Through west, central and south Europe, extending northwards to the Faeroes, Denmark, South Sweden, Gotland, Oesel; and eastwards to Dantzig, Vistula and Danube Delta; North Africa, Asia Minor (compare *J. sylvaticus* which extends rather less far to the north, but farther east, to Moscow).

A lowland plant. No definite record of upper limits in Britain, but probably ascends no higher than about 500 ft.

In Tyrol it reaches *c.* 2460 ft. (750 m.) (Graebner, 1909); in Graubünden 3608 ft. (1100 m.) (Braun-Blanquet & Rübel, 1932).

II. *Habitat.* Occurs in fens and marshes, perhaps only where the groundwater is alkaline; especially characteristic of calcareous peat. Apparently tolerating moderate concentrations of sea salt, since it frequently occurs in brackish marshes near the coast (Kent, Devon, Dorset, Cork, Kerry) and inland (Marcham, Berkshire). Dominant over extensive areas of calcareous fen peat in East Anglia and elsewhere. Also in river valleys, around ponds and lakes, near calcareous seepage lines and springs and in dune slacks. Apart from East Anglian fens and central limestone area of Ireland, a rare and local plant. Thus, in Oxford district, occurs in small calcareous fens, at seepage lines where Corallian Beds overlie Oxford Clay, very locally beside rivers and streams, and in salt meadows near Marcham, Berkshire; in the Cambridge district it is almost, but not quite, confined to the main fen area and small outliers such as Dernford Fen; and on Cavenham Heath, Breckland, it is strictly confined to alluvial soils of stream valleys where it forms extensive nearly pure communities. Usually on peat, but may occur on alluvium or sand. Most luxuriant where the water-table is close to the surface or a few inches above it throughout the year; may persist where drainage has brought about a fall in the summer water-table. Winter flooding may occur, but is certainly not essential.

In colonization of bare sloping peat margin of experimental pond at Wicken Fen, Cambs., *J. subnodulosus* formed a dense zone of tall plants on soil about -4 to $+2$ in. (-10 to $+5$ cm.) in relation to pond water-level which varied only a few cm. during the year. This zone was between luxuriant *Cladium* growth on deeper side and *Phalaris arundinacea* on shallower side, but scattered *Juncus* plants were growing both above and below zone of (? temporary) dominance. Probably *Juncus subnodulosus* occupies somewhat higher levels than *Carex stricta* (*C. elata*) and with this may replace Cladietum as early stage in deflected succession when Cladietum is suppressed by frequent cutting. Preliminary levelling in Wicken Poor's Piece suggests lower limit of colonization where depth of standing water is between 2 and 10 in. (5 and 25 cm.) in winter, water-table falling to 10 in. (25 cm.) or more below surface in summer. In Molinieta, *Juncus subnodulosus* occurs where summer water-table may sink to about 20 in. (50 cm.) below surface (Godwin & Bharucha, 1932). Glück (1936) records typical form in 1–14 in. (2·5–40 cm.) standing water and a sterile *forma submersus* from clear flowing water in Bavaria.

*p*H above 7·0 in great majority of English habitats. In Oxford district, *p*H records colorimetrically determined in eight habitats showed range 7·0–7·9 (Cruttwell). Reported by Praeger (1934) to grow in acid soil and water near Roundstone, Connemara. Compared with *J. articulatus* and *J. sylvaticus*, its ecological range is very restricted and well defined. Little tolerance of shade. May persist in non-flowering condition under light shade of open willow carr, but disappears as canopy closes. 'Nowhere in Wicken Fen does *J. subnodulosus* persist in young scrub of Franguletum alni' (Godwin).

III. *Communities.* As a result of its very narrow habitat range, all lists of communities in which *Juncus subnodulosus* is dominant or abundant have strong floristic similarities. The following species occur in five or more of nine stands with *J. subnodulosus* dominant on calcareous peat near Oxford: *Mentha aquatica, Angelica sylvestris, Galium uliginosum, Carex panicea, Lotus uliginosus, Scabiosa succisa, Valeriana dioica, Orchis Fuchsii, Festuca rubra, Filipendula Ulmaria, Cirsium palustre, Equisetum palustre, Hypnum stellatum* and *H. cuspidatum.* Other species are restricted, near Oxford, to this community and to those, also on calcareous peat, in which *Juncus subnodulosus* is an abundant associate of *Phragmites, Schoenus* or *Molinia*: *Cirsium pratense, Parnassia palustris, Oenanthe Lachenalii, Anagallis tenella, Epipactis palustris, Orchis praetermissa, Eriophorum latifolium, Carex lepidocarpa, C. rostrata, C. fulva, C. pulicaris.* 'Mowing marshes' round Calthorpe Broad, Norfolk (Godwin & Turner, 1933) have *Juncus subnodulosus* very abundant with *Phragmites, Carex elata, Comarum palustre, Hydrocotyle* and *Carex panicea* all abundant and *Pedicularis palustris, Schoenus nigricans, Hypnum stellatum, H. cuspidatum* and *Aneura pinguis* as prominent associates. The list from wettest parts of seepage zones with shallow calcareous peat is practically the same; while that from humus-rich alluvium near Oxford differs chiefly in the absence of *Schoenus* and *Molinia* and of species listed above as confined to calcareous peats.

IV. *Response to biotic factors.* Very tolerant of frequent cutting or burning and of grazing. At Cothill, Berkshire, it is dominant or abundant in areas which have been cut or burned annually; near Calthorpe Broad, Norfolk, Godwin and Turner record it as very abundant or co-dominant in the 'mowing marshes' which are 'cut from time to time' and co-dominant in 'rough meadows pastured by horses and cattle'; and at Wicken Fen, Cambridgeshire, it reaches its greatest abundance in the 'litter' community (Molinietum) which is cut yearly. Its tolerance of frequent cutting gives it an advantage over taller, less tolerant species such as *Phragmites* and *Cladium*, to whose competition it is so sensitive that it 'becomes on Wicken Fen an indicator species for the Molinietum produced by yearly cutting' (Godwin). 'It appears to maintain itself there, although apparently less well able than *Carex panicea* to pierce the *Molinia* tussocks with its rhizomes and young shoots' (Godwin, 1941). In sample plots of Cladio-Molinietum, cut on varying rotations from 1927 to 1940, *Juncus subnodulosus* increased from rare to locally abundant where cutting was once yearly, but remained rare on uncut areas (Godwin, 1941). Survives fen fires, easily regenerating both by seed and rhizomes. It appears that *J. subnodulosus* plays an important role only in fen successions which are deflected by cutting, grazing or burning (cp. *Molinia*).

Displaced by *Juncus articulatus* on well-trodden paths and droves.

V. (*a*) *Gregariousness.* Growth is not tufted, but the plant may form extensive almost pure communities in which the maintenance of dominance may depend largely on the very heavy mat of lodged and dead shoots. Where it is not dominant it is represented by scattered shoots in the mixed vegetation.

(*b*) *Performance in various habitats.* At Cothill, Berkshire, mean shoot heights in 1940 varied from 27 in. (68·5 cm.) in dense *Phragmites*, in 2 in. (5 cm.) standing water, to 37·5 in. (95 cm.) in pure Juncetum in 6 in. (15 cm.) of standing water, unshaded; and to 42·5 in. (108 cm.) under light shade of sparse *Phragmites* with water-table at the surface. There were no flowering shoots in young willow carr or in dense Phragmitetum and flowering was best in the open.

(*c*) *Effect of frost, drought, etc.* For sensitivity of seedlings to freezing, etc., see under *Juncus inflexus*.

VI. (*a*), (*b*) *Morphology.* A far-creeping rhizomatous plant (see introductory notes on *Juncus*). Rhizomes long, often reaching many feet and where the plant is dominant forming a dense mat about 2–3 in. (5 to 7·5 cm.) below surface. Rhizome sympodial, with renewal bud in axil of second scale of segment. Erect shoots ½–1 in. apart on main sympodium. Lateral spur-shoots, also sympodial, arise in axils of third scale of segments in small groups of 2–6 alternately to left and to right of main sympodium, groups being separated by lengths with no spurs. Spurs with crowded erect shoots only *c.* ¼ in. apart. Flowering shoots have 3–5 basal scales, and usually two foliage leaves with long terete laminae. Pith of leaves with both longitudinal and transverse septa, latter not all at same level. (Contrast *J. sylvaticus* and *J. articulatus* with no longitudinal partitions.) Laminae at first rigid and held almost vertical. Sterile shoots with basal scales and a single long cylindrical stem-like leaf as in Junci genuini. Two kinds of adventitious roots borne on rhizome:

stout straight unbranched roots growing vertically downwards to depth of 6–9 in. (15–22 cm.) below surface; and slender, much-branched roots directed sideways or upwards. Roots of both types covered throughout their length with persistent root-hairs.

(*c*) *Mycorrhiza.* No information.

(*d*) *Perennation.* Semi-rosette hemicryptophyte. Sterile shoots emerge in autumn and remain green throughout winter. In autumn, too, flowering shoots fall over and turn brown so that they contrast strongly with erect, fresh-green sterile shoots which have pierced the mat. Flowering shoots emerge in spring from buds which have remained just below surface of substratum during winter.

(*e*) *Vegetative reproduction.* By rhizome extension. Very rapid when colonizing in shallow water over peat; but much less rapid in drier situations. New colonies may be formed by pieces of rhizome being torn off and carried away during break-up of ice in spring (Graebner, 1909).

(*f*) *Longevity.* No information.

(*g*) *Age at first flowering.* No information.

(*h*) *Frequency of seed production.* Apparently sets seed every year in the south, but not in north England.

(*i*) *Ecotypes.* No evidence.

(*j*) *Chromosome number.* $2x=40$ (Timm; material from Cothill, Berks.).

VII. *Phenology.* (*a*) New roots appear, some in autumn and some in early spring.

(*b*) Sterile shoots arise in September and October and flowering shoots in April and early May, Oxford district.

(*c*) Flowers in July and August, later than *J. inflexus* and *J. effusus*, but perhaps slightly earlier than *J. sylvaticus.* Often does not flower in north England till late August or early September, and frequently fails to set seed (Pearsall).

(*d*) Seeds probably shed mainly in September and October.

(*e*) Germinates in cultivation in April and May. No data for naturally occurring seedlings.

VIII. (*a*) *Mode of pollination.* Wind-pollinated; protogynous.

(*b*) *Insect visitors.* No information.

(*c*) *Cleistogamy.* Not reported.

(*d*) *Apomixis.* Almost certainly amphimictic.

(*e*) *Vivipary.* Proliferating form reported by Godwin from Wicken Fen, Cambridgeshire (see Glück, 1936).

(*f*) *Hybrids.* No hybrids are known.

(*g*) *Amount of seed.* No information.

(*h*) *Dispersal.* Seeds not mucilaginous and not sticking together in groups. Probably dispersed by scattering and perhaps to some extent by water. In one experiment, of ten seeds freed from superficial air-films, seven were still floating on the following day.

(*i*) *Viability.* Seeds did not germinate after 8 years in the laboratory.

(*j*) *Conditions for germination.* Freezing unnecessary. Seeds collected in autumn and sown on filter-paper in following spring germinated only in light. High mortality of seedlings under laboratory conditions, with high incidence of chlorosis.

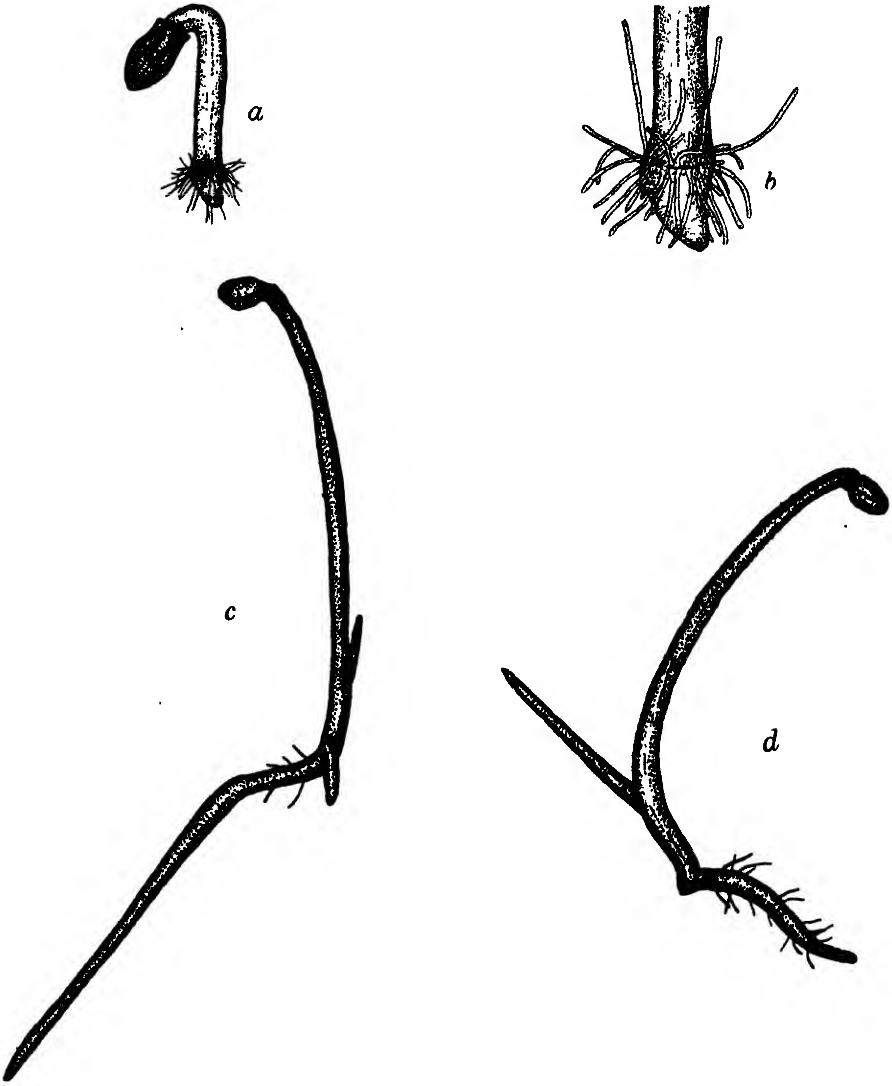

Fig. 2. Stages in germination of *Juncus subnodulosus.* Seed sowni n laboratory. (*a*) 7 days after sowing; × 20. (*b*) 7 days after sowing, showing circlet of root hairs at base of cotyledon; × 40. (*c*) 16 days after sowing; × 10. (*d*) 21 days after sowing; × 10.

(*k*) *Morphology of seedlings.* See introductory notes on *Juncus* and Fig. 2. The cotyledon erects sooner than in Junci genuini.

(*l*) *Effective reproduction.* Both vegetative and by seed. On Wicken Fen spreads very rapidly by seedlings into areas with bare soil exposed either as a result of felling fen scrub with sparse undergrowth or clearing by fire, or clearance and repeated cuttings of Cladietum and Cladio-Molinietum in carr in making new fen-droves (Godwin).

IX. *Parasites: diseases.* See introductory notes on *Juncus.* The rust *Uromyces Junci* (Desm.) Tul., with aecidial stage on *Pulicaria dysenterica*, has been recorded in Britain only on *Juncus subnodulosus.*

X. *History.* No information.

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